

Predation and social behaviour in a
population of domestic cat.
An evolutionary perspective.

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PREDATION AND SOCIAL BEHAVIOUR IN A POPULATION OF DOMESTIC CAT.
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LIST OF PAPERS

This thesis is based on the following papers, which will be referred to by their Roman numerals.

- I Liberg, O. 1980. Spacing patterns in a population of rural free roaming domestic cats. *Oikos* 35: 336-349. Reprinted by kind permission of *Oikos*.
- II Liberg, O. Food habits and prey impact by a rural domestic cat population in southern Sweden. Manuscript.
- III Liberg, O. In press. Hunting efficiency and prey impact by a free roaming house cat population. Proc. of the XIVth Int. Congr. Wildl. Biol., Dublin 1979. (In press.)
- IV Liberg, O. Courtship behaviour and sexual selection in the domestic cat. Manuscript.
- V Liberg, O. Reproductive success in male cats in relation to social status. Manuscript.



PREFACE

When I switched from my profession as a veterinarian to start studying vertebrate ecology because of a genuine interest in wildlife, I was not too pleased being asked by my supervisor Sam Erlinge to direct my efforts towards cats. To me, that seemed as going back into the domestic sphere again. Many people, including myself, had hard to see that anything could be learned about wild carnivores by studying domestic cats. I changed my mind during the years to come. Cats offer some unique possibilities of insight into aspects of behavioural ecology of felids, virtually impossible to obtain from populations living in the wild. I am only afraid I have not used these possibilities enough.

I really have enjoyed my time working with this thesis. An important contribution to this was the opportunity to work together with the members of the Wildlife Research Group, together with other colleagues and staff at the Department of Animal Ecology, together with a number of interested and able field assistants and last but not least with all the cooperative and hospitable owners of cats in the Revinge area.

Especially I would like to thank Per Brinck, the Head of the Department of Animal Ecology, who offered encouragement and facilities, and Sam Erlinge, my supervisor, whose generous support and constructive criticism all through my work was invaluable. For aid in the field and criticism and comments on my thoughts and papers, I thank Gunilla Andersson, Catharina Cederlund, Claes Ericsson, Görgen Göransson, Sven-Olof Fransson, Anders Johansson, Sven Lundberg, Ingvar Nilsson, Daniel Palmgren, Birgitta Persson, Torbjörn von Schantz, Ulla Steinwall, Håkan Welff and Anders Wetterin. To Jon Loman I would like to direct a special thank for his genuine interest in cat sociobiology, and thereof following keen field observation and discussions, and for his skillful work with computer programs.

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Many other people, both in my near social surroundings, and in the professional sphere, were of great help. All these are deeply thanked.

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SUMMARY OF THE RESULTS, AND DISCUSSION OF ADAPTATIONS OF THE CAT TO SYMBIOSIS WITH MAN

According to modern evolutionary theory social organization of animal populations is strongly influenced by environmental factors like the dispersion, abundance and predictability of food, predation pressures and competition from other species (e.g. Crook 1964, Crook & Gartlan 1966, Hamilton 1971, Alexander 1974). Rather detailed hypotheses have been put forth to explain the evolution of social factors such as territorial defense, group size, parental care, mating systems and cooperation (e.g. Brown 1964, Brown and Orians 1970, Clutton-Brock and Harvey 1976, Emlen and Oring 1977 and Emlen 1978).

In this summary, I will use this theoretical background to interpret the results of papers I-V. Further I will try to outline some of the selection pressures and point out some adaptations that characterize the evolution of the domestic cat, Felis catus.

SOLITARY AND GROUP-LIVING FELIDS

The wild ancestors of the domestic cat are one or several of the small Old World felids being subspecies of Felis silvestris (Zeuner 1963, Kratochvil et al. 1976, Corbet 1978, Todd 1978). These ancestral felids fed on dispersed, moderately abundant and predictable prey (Ewer 1973, Corbett 1979) and should according to evolutionary theory in sociobiology be solitary, defend feeding territories and have a monogamous or weakly polygynous mating system, (Kleimann and Eisenberg 1973, Clutton-Brock & Harvey 1978).

Very little is known about social behaviour of small felids in the natural state, but the data available fits the theory rather well. The European wild cat Felis silvestris lives a solitary existence except during breeding. Females have home ranges exclusive of other females, but overlapping with those of males (Corbett 1979). Similar spacing patterns have been described for Lynx lynx (Haglund 1966) and bobcat Lynx rufus (Bailey 1974). For the latter species it was shown that one male might overlap the home range of several females.

In the examined rural population of domestic cats in the Revinge area in Southern Sweden, it was shown that female cats lived alone or in groups of 2-7 adult females at human households (Paper I). The females in a group were closely related as female offspring stayed with the group, and foreign female cats were not tolerated. Few of the females ($< 15\%$) emigrated from their natal groups. Emigrating females always settled at a new human household, where no other adult female cats were resident. Most male cats dispersed, probably in response to aggression from older or more dominant males (Paper V). Usually dispersing males settled as feral cats, subsisting mainly on natural prey (Paper I, II, III).

Females had small communal group home ranges (40-50 ha), not overlapping with those of other female groups (Paper I). Males had larger home ranges than did females. Old males occupied home ranges up to 900 ha (Paper I, V). Home ranges of different males overlapped partly or completely (Paper I, V). This spacing pattern is similar to that reported for other rural domestic cat populations (Laundré 1977, Macdonald and Apps 1978, Corbett 1979). All these populations were fed and housed by their human owners, but did also hunt for themselves, as was the case for the Revinge population (Paper II, III).

A high-density, feral and urban cat population living in the dock yards in Porthsmouth, U.K. also was organized in female kin groups, and group members shared the defence of one or several concentrated food resource like garbage bins (Dards 1978)

In contrast to these human supported cat populations, feral cat populations that lived in rural or wilderness areas and fed entirely on natural prey usually were solitary (Derenne 1976, van Aarde 1978, Corbett 1979). In at least one case, it was shown that females not only lived alone, but had exclusive territories (Corbett 1979).

What is the adaptive value of group-living for domestic cat? Alexander (1964) argues that there are three main selection pressures favouring group living: 1) Anti-predator advantages, 2) the nature of food resources disfavours "splintering of the group" and 3) extreme localization of some critical resource such as safe sleeping places. The anti-predator argument does not provide a satisfactory explanation. I never observed communal defence against a predator by cats, nor has such behaviour been reported in the literature. The dilution or "selfish herd" argument does

not seem to fit the cat case (Hamilton 1971, Bertram 1978). However, it could be, that the protection the human settlement offers against wild predators, has released the cats from predator pressure, that prevented group living in the original state of the cat. The food argument seems more appropriate. The human settlement offers a clumped and abundant food resource, that allows for group living. It is interesting to note that domestic cats that secondarily have gone feral, revert to the original solitary way of life. This implies a great deal of flexibility in the social behaviour of the domestic cat, a feature also pointed out by Corbett (1979).

The argument of the localization of a critical resource might have some application. In northerly climates, the buildings of human settlements might provide important shelter against adverse weather especially during winter, but this does not explain social groups in warmer climates.

Therefore, clumped food resource offered at human settlements seems to be the most important selection pressure behind group formation in the domestic cat. For the only other true group-living felid, the lion, Panthera leo, also the nature of food has been proposed to be the most important selection pressure for living in groups (Kleimann and Eisenberg 1973).

NATURAL PREY AND FOOD DERIVED FROM HUMAN HABITATION

Even if cats are fed satisfactorily by humans, they continue to hunt and feed on wild prey (Paper II, III, George 1974, Corbett 1979). In the Revinge area, the main prey of the cats were rabbits Oryctolagus cuniculus, and field voles Microtus agrestis. House-based cats obtained half of their food from their own hunting during summer, and 10-20 per cent during winter. The remaining food was given by humans. However, when availability of rabbits increased drastically because many of them were starving during a period of severe winter weather, cats responded strongly, and changed their diet almost completely to rabbits.

The advantage for cats to retain their hunting ability is obvious: By its own hunting the cat has increased its energy input, and kept itself independent of fluctuation in the human subsidies

The diet of feral male cats in the Revinge area had almost the same composition of natural prey as house-based cats, although with a weak tendency toward more rabbits and less rodents (Paper II, III). Thus, feral cats have a similar food niche as domestic cats. Competition for food might be high in times of

prey shortage, and should disfavour feral cats most, as these cats do not have the provisioning by humans to rely on. This could help to explain why there were no feral female cats in the Revinge area, and why feral population of cats in general seem to occur mainly in areas where there are no house-cat populations, (urban areas are excepted) (Coman et al. 1972, Derenne 1976, Jones 1977, Fitzgerald et al 1979, Corbett 1979). Female feral cats that have to bring food to kittens, would be more vulnerable to this competition, than males, that only have to hunt for themselves. In urban areas, cats are mainly scavengers, which makes the situation there different (Dards 1978, Todd 1978).

Abundance of natural prey had an influence on dispersal tendency in male cats in the Revinge area. As already mentioned, dispersing males usually settled as feral cats, for which wild rabbits were a critical food resource. In 1973-76 rabbits were abundant in the Revinge area, but in winter 1977 a serious decline in rabbit population started. This decline continued till the study ended in 1981 (Paper III). Feral cats had a significantly lower intake of natural prey after the winter 1977 as compared with the period before (Paper III and Table 1). Likewise the average weight of male feral cats decreased after this winter (Table 1).

TABLE 1

Daily prey intake per cat and average bodyweight for male feral cats in the Revinge area, before and after the rabbit decline in winter 1977.

T-tests of difference in prey intake based on monthly sample means.

	Before rabbit decline	After rabbit decline had started	t-tests (one-tailed)
Daily intake of prey/cat (g)	330	170	t = 1.9, df = 28 p < 0.03
Average body- weight (kg) of cats	4.5	3.8	t = 3.4, df = 29 p < 0.001

Obviously, at least some feral cats had difficulties maintaining themselves on natural prey, when rabbits declined. This was the most likely reason for an increased tendency in males to stay in the households where they were born. In 1974-77, mortality and

emigration reduced the number of male cats in the households, so that only one out of fifty males reached the age of 3.5 years while still in his original household, and none reached the age of four (Table 2). After 1977, six males out of thirty-eight

TABLE 2

Age structure of male cats staying in their natal households, in two periods.

Number of male cats that reached the age while still in their natal household	Period	
	1974-77	1978-81
1 year	50	38
1.5 "	27	28
2 "	22	22
2.5 "	12	15
3 "	7	6
3.5 "	1	6
4 "	0	4
4.5 "	0	3
5 "	0	2
5.5 "	0	1

still occurred in their natal households at the age of 3.5 years, four males reached the age of four years and one even reached the age of 5.5 years while still in his natal home. Furthermore, in 1974-77, four different post-dispersed feral male cats were recorded to have obtained Breeder status (see below), but no male attained that status while still living in his natal household. Conversely, in 1978-81 only one feral male attained Breeder status, but four males that had stayed in their original homes had reached that stage. In Paper IV and V, it was stated that body-weight was an important factor determining social status. Obviously feral males had difficulties in gaining the weight necessary to attain a high social rank. This illustrates some of the complicated interactions between the different food resources available to domestic cats, and the social behaviour of these cats. There might have been selection and counter selection for the same adaptation at different times and different places during the evolution of the domestic cat.

Male cats in the Revinge area competed intensely for mates. A small number of male cats, called Breeders, maintained mating priorities, each Breeder controlled one or several female groups (Paper V). Often several males participated simultaneously in courtship of a female in oestrus. There was always one male that was clearly discernable and stayed close to the female in oestrus and performed all copulations. This male occupied the Central Male position (CM). Usually the CM position was held by the Breeder of the courted female's group. Other males present occupied more peripheral positions called Peripheral Male position (PM) (Paper IV).

Males went through a series of life stages. They were called juveniles up to the age of 8-14 months, then they rather abruptly became the targets of aggressive attacks by older males (Paper V). After this the young adult male was called a Novice.

Many Novices emigrated. Males that emigrated were called Outcasts if they followed the typical pattern, and settled in areas away from the near neighbourhood of dominant male cats.

Both Novices and Outcasts avoided contact with dominant male cats. Not all Novices emigrated, however, those that did not eventually entered the next life stage, the Challengers. Outcasts also eventually became Challengers. Usually this occurred at an age of two to three years. Challengers participated in courtships as PMs, and they did not always try to avoid encounters with Breeders. Challengers became more involved in overt aggressive interactions than did Novices and Outcasts. Usually Challengers attained Breeder status at the age of three to four years. All categories of male cats mated with females, but the reproductive success of Breeders was twice as high as Challengers, and four times higher than Novices and Outcasts (Paper V).

These aspects of social life has not been described for domestic cat before. For wild small felids, details of competition for mates, dominance relationships, courtship and differential reproductive success of males are virtually unknown. However, it is probable that competition among males for mates is more intense in the domestic cat, than in any solitary wild felids, as a consequence of the aggregated distribution of female domestic cats (Emlen and Oring, 1977). It is, therefore, believed that the reproductive behaviour observed of male cats is an adaptation

to the domestic situation, caused by an increased intrasexual selection. There has not been any obvious morphological adaptations such as the mane in the male lion (Schaller 1972). In the lion, another effect of intrasexual selection is the occurrence of male coalitions to increase competitive ability (Bygott et al. 1979). In Paper I, I argued that this has not evolved in domestic cat, for the reason that cats don't hunt cooperatively, and thus lack a necessary prerequisite for other types of cooperation. However, if there really had been a strong selective advantage for male coalitions in the cat, there would not have been needed such a prerequisite. Most likely there is some other selective pressure against coalitions. Maybe the female groups generally have been too small and scattered to make them profitable for two or more males to share.

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Spacing patterns in a population of rural free roaming domestic cats

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Spacing patterns in a population of domestic and feral cats in a rural area in southern Sweden were investigated by visual observations, trapping and radio tracking. Females lived alone or in groups around human households. Within each female group the home ranges almost completely overlapped, but between different female groups there was little or no overlap. Most females remained in the same place all their lives, but a few individuals moved and became established at new households, invariably one where there were no other female cats.

There were always six to eight feral, well established males in the area, with moderately overlapping home ranges. These ranges were considerably larger than those of females, and one male might include several female groups within his home range. Young males, born in the area, stayed with the female group, where they were born until they were 1.5–3 yr old. They then left and tried to settle somewhere else. Spacing patterns in this cat population can be explained by the influence of proximate and ultimate factors, among which intraspecific aggression and adaptation to living in human households are the most important. Parallel evolution of lion and house cat social organizations is discussed.

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Характер прерывистого распределения популяции домашних и диких кошек в сельской местности южной Швеции изучали путем визуальных наблюдений, отлова и радиослежения. Самки живут в одиночку или группами вокруг жилья человека. Внутри каждой группы самок домовые участки почти полностью перекрываются, но между отдельными группами перекрывание отсутствует или незначительно. Большинство самок остается на одном месте в течение всей своей жизни, но некоторые особи мигрируют и обосновываются у новых жильцов, но неизменно там, где нет других самок. На одном участке всегда имеется 6–8 диких котов с умеренно перекрывающимися домовыми участками. Эти участки значительно больше, чем у самок. Участок одного самца может включать территории несколько их групп самок. Молодые коты, родившиеся в определенном участке, остаются в группе самок, где они родились до 1,5–3-летнего возраста. Затем они покидают его и основывают свое поселение в другом месте. Прерывистый характер распределения в данной популяции кошек может быть объяснен влиянием проксимальных и ультимативных факторов, среди которых наиболее существенны внутривидовая агрессия и адаптация к обитанию в жилищах человека. Обсуждается параллельная эволюция социальной организации у львов и домашних кошек.

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1. Introduction

Spacing in animal populations is determined by social organization and by the environment. Understanding of the spacing systems of free living carnivores, is dependent upon information of the different individuals' social status. This kind of information is often very difficult to get when studying wild carnivores. Studies of these aspects of domestic cats offer great advantages. In many ecological and behavioural aspects, free roaming domestic cats (*Felis lybica f. catus*) resemble much of true wild carnivores, and probably also stand closer to their wild ancestors than any other of our common domestic animals. At the same time the cats' close connection to humans makes close observation possible without disturbance. However, most studies on free ranging house cats have dealt with food habits (e.g. Hubbs 1951, Coman and Brunner 1972, Heidemann 1973, George 1974), Baron et al. (1975) and Leyhausen (1965) studied the social behaviour of cats under laboratory conditions. Leyhausen and Wolff (1959) and Laundré (1977) also observed behaviour and social interactions in single groups of free ranging cats. A few studies have included a whole feral cat population, e.g. Derenne (1976) and Jones (1977), but their emphasis was on feeding and hunting behaviour, and few details of social behaviour were given.

The object of this study was to examine the distribution and movements of the cats in a rural, free roaming population. It is one part of a long term study on the ecology of the rural domestic cat in southern Sweden. The study is part of a team project analysing the regulatory mechanisms in a predator-prey community.

2. Study area

The study was carried out in the Revinge area in Skåne, southern Sweden. The area was previously cultivated, but in 1965 it was turned into a military training area. Cultivation ceased, and the area is used for military training, and cattle grazing. The many small farms were either abandoned or used only as living quarters, the outbuildings being either deserted or used as military stores. About 10% of the area is marsh or wet meadow, where the most abundant cat prey is the field vole *Microtus agrestis* L. Dry sandy hills, partly planted with pine, occupy large areas. This habitat is densely populated by rabbits, *Oryctolagus cuniculus* L. Small woods and stands and lines of deciduous trees are scattered all over the area. About half of the area consists of grazed or mowed fields (Fig. 1).

3. Material and methods

Contact with households. Households with cats provided information on their own cats, as well as on visiting

foreign cats. All cats in the area were given an individual number in a diary, where all important events in the life of each cat were noted. Cats that lived in the area when the study started in 1973 were numbered between 1 and 99. Cats born in 1974 were numbered 101–199, those born in 1975 201–299 etc. Cats that immigrated into the area after 1973, were numbered from 801. The households will be referred to with letters (Fig. 1).

Identification and classification of cats. The natural coat colour of all cats were drawn on a standard form to facilitate identification in the field. Tabby and black cats without white markings were difficult to identify from a distance. Some of them were marked with small metal ear markers, collars or by ear-clipping. At anyone time a small number, mostly below 10% of the population, could not be identified individually in the field.

Cats were classified as house cats when they were regularly fed in one or several households. Cats without such connections were called feral. Cats observed in the study area only once, or several times during a period shorter than one month, were regarded as transients. It was usually not possible to determine whether such cats were house cats or feral cats.

Observations. Distribution and home ranges of individual cats were determined mainly by direct visual observations in the field with ordinary field glasses. Cats were observed during daytime from a car, or while I was walking or riding on horseback through the area. Whenever a cat was spotted, identity (if possible), date, time, location and type of activity was noted. I then followed the cat as long as possible, without disturbing it, noting details of its movements and activities. A total of 104 hours of direct observations were obtained. During nighttime I searched for cats with a strong mobile beamlight along a standard route. I also made observations when radio tracking cats. In total 617 observations of 109 different individuals were made in the field. Beside these, 85 observations were made, where the cat observed could not be identified.

Trapping. Trapping was performed irregularly for short periods during 1974–1977 to mark feral cats and equip them with radio collars. Trapping provided some data on distribution. Double door box traps, 15 × 20 × 200 cm, baited with fish or rabbit meat were used. In 960 trap days, 79 cats were trapped 88 times. Retrapping of the same individual was rare; one cat was trapped four times, and six cats were trapped twice; the rest only once each.

Radio tracking. Radio tracking gave detailed information on movements and home ranges of some individuals. The collar-transmitters, (Tester et al. 1964) weighed 70–85 g, i.e. about 2% of the cats' body weight. Battery life was up to five months, although most transmitters did not work for so long. A single

portable receiver with a loop antenna was used. Average range of reception was 300 m, although occasionally signals could be detected from a distance of up to 800 m. When tracking cats, I tried to distribute the radio locations evenly over the day, but there was a bias for diurnal locations. In some cases cats were tracked continuously for several days, providing information on activity and movement patterns. Data from 3116 radio locations of 24 different individuals (12 females and 12 males) have been included here.

Delineation of home ranges. The boundaries of the home ranges were mostly drawn according to the convex polygon method (Mohr and Stumpff 1966). However, information on the movements of cats and of topography and vegetation were sometimes included to modify the form of the home ranges with respect to the use of the area by cats.

Population data. Data on the density of cats and other population variables were obtained from the cat owners, from trapping and from visual observations. To compare the population density in the study area with that of the surrounding agricultural land, road counts were performed during two nights, when the number of cats observed in the lights from the car per 100 km of driving was used as an index of cat density.

4. Results

4.1. Population characteristics

The number of cats in the study area was 55–72 individuals during the study period (Tab. 1), i.e. a density of 2.5–3.3 cats km⁻². This is a low value compared with the surrounding agricultural land. The number of cats observed in the Revinge area per 100 km road drive during a two night census in August 1975 was only two individuals, as compared with 20 seen per 100 km in the surrounding area.

The sex ratio of the population was uneven, with a surplus of females, viz. 63 males: 100 females. In the first year-class, the ratio was almost even, 90: 100, but then the proportion of males dropped off. In the households, I never found males older than 3.5 yr; females sometimes reached an age of 10 yr or more (Tab.1).

Only about 10% of the resident population was feral. This percentage was almost constant during the study period, but as there was some turn over, the total number of feral cats recorded was seventeen. Only one of the feral cats was female. Eighteen transient individuals were recorded. Some of these might have been feral animals resident on the margins of the study area.

4.2. General distribution of females

All female cats except one were associated with human households, and the distribution of female cats followed

Tab. 1. Composition of the Revinge cat population by 1 April 1974–1977.

		1	2	3	4	Age, yr		7	8	9	10	Unknown >10 age	Σ	♂/♀	Tot. pop.
						5	6								
1974	♂	14	5	1	—	—	—	—	—	—	—	—	20		
Domestic	♀	12	8	3	3	4	3	1	2	—	1	2	39		
														26/39	65
Feral	♂	—	—	—	—	—	—	—	—	—	—	—	6	6	
	♀	—	—	—	—	—	—	—	—	—	—	—	—	—	
1975	♂	14	8	3	—	—	—	—	—	—	—	—	25		
Domestic	♀	17	7	5	—	1	3	2	1	2	—	3	41		
														31/41	72
Feral	♂	—	—	—	—	—	—	—	—	—	—	—	6	6	
	♀	—	—	—	—	—	—	—	—	—	—	—	—	—	
1976	♂	8	5	1	—	—	—	—	—	—	—	—	14		
Domestic	♀	7	12	4	2	—	1	—	2	—	2	2	33		
														21/34	55
Feral	♂	—	1	1	1	—	—	—	—	—	—	—	4	7	
	♀	—	—	—	—	—	—	—	—	—	—	—	1	1	
1977	♂	13	1	1	—	—	—	—	—	—	—	—	15		
Domestic	♀	19	6	11	—	2	—	1	—	1	—	2	45		
														22/45	66
Feral	♂	1	1	1	—	—	—	—	—	—	—	—	4	7	
	♀	—	—	—	—	—	—	—	—	—	—	—	—	0.63	

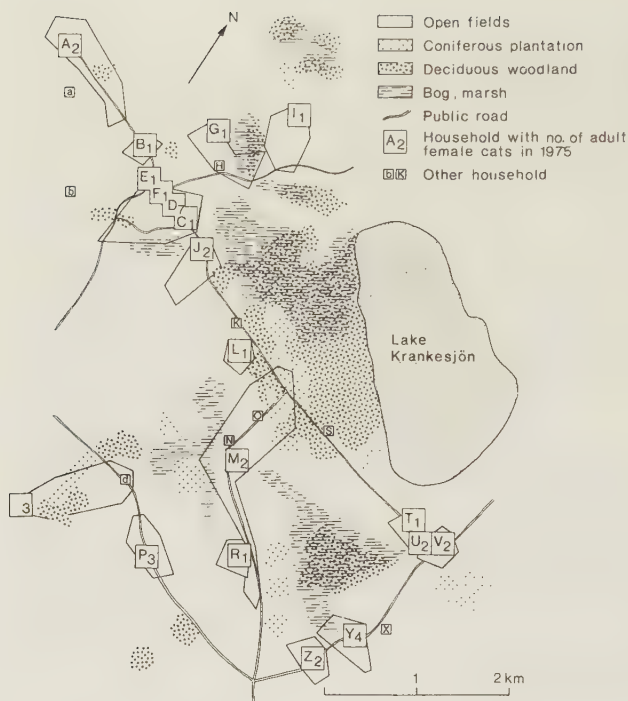


Fig. 1. Distribution of female cats in the Revinge area in April 1975. The communal home range for each female group is outlined. The delineations of the home ranges were based on visual observations, and in some cases radio tracking, 1975 to 1977.

that of human settlements (fig. 1). The female cats lived alone or in groups of up to eight adults. Usually all the group members were closely related. In the group of household D all the cats descended from two sisters, born in 1964 (Fig. 2). Besides adult females of all ages, a group of domestic cats could contain adult males up to 3.5 yr old, as well as juveniles of both sexes.

The female home ranges were small, up to 30–40 ha, and the animals seldom moved further than 600 m from their home farm (Fig. 1). Occasional movements up to 1800 m were recorded. Besides the households where the females were resident (primary homes) the cats often had one or several buildings within their home range, which were regularly used for shelter and rest. These places (secondary homes) could be barns or similar buildings up to 800 m away from the primary home.

The distribution of females was clumped. Large areas of apparently suitable habitat were unused by female cats, as the groups utilized small home ranges and were connected to households (Fig. 1).

4.3. Female dispersal, and changes of home ranges

Most female cats remained throughout their lives in the home where they were born. However, a few emigrating females were recorded (Tab. 2, Fig. 3). Their case histories are as follows:

Female 113 was born to ♀30, belonging to household D (Fig. 2), at an unknown place outside the household, in summer 1974. She was brought home by her mother in October, as the only kitten of that litter. By that time there were four adult females, two other juvenile females and one juvenile male in the household (Fig. 2). Female 113 was never accepted by the other cats; one of the juvenile females behaved especially aggressively towards her. In June 1975 ♀113 left her home, but returned for short visits a couple of times in July. In autumn 1975 she lived as a feral cat in the area outside the range of her native group. She used a much larger area than domestic cats usually do (Fig. 3b). Her range partly overlapped the home ranges of the adult females 41 and 61, but she never entered the core areas around their primary homes (household G and I respectively). At household H, having no cats at that time, the people noticed the visiting cat, and started to feed her. Gradu-

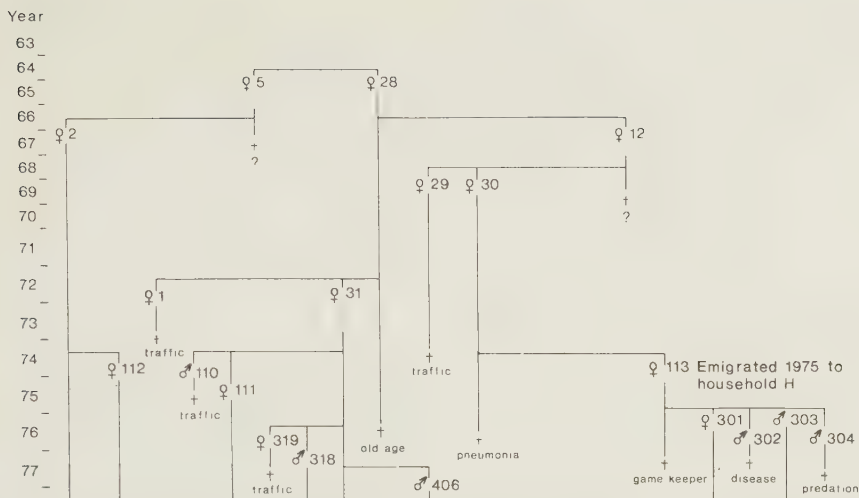


Fig. 2. Family relations of cats in household D, illustrated as a genealogical tree. Vertical lines indicate cats' life span. Horizontal lines give connection mother-offspring. Causes of mortality are given. Not all the cats that have lived in the group are indicated in the figure, as reliable data are missing on cats that died before 1973, when this study started.

ally the cat got familiar with her new home. In spring 1976 she again behaved as a house cat. She reduced the size of her home range, but included the home range of the female 41, which had died in late autumn 1975 (Fig. 36).

Female 135 was born in 1974, and was imported as a kitten to household J together with female 134, who was of the same age but unrelated to 135. In summer 1975 when female 135 had kittens, she gradually became more aggressive towards female 134, and in August she moved with her kittens to household K (Fig. 3A) where she settled. At K there were no cats at that time. Female 135 was still living in her new home in autumn 1977.

Female 220 was born 1975 in household M, and was moved as a small kitten by her mother to the neighbouring household N, and was left there while the mother returned to M. The kitten was fed by the people at N, and stayed there. In spring 1976 she had a litter. In summer and autumn that year she spent an increasing amount of time away from N, and frequented the area around the abandoned farm U (Fig. 3A). There she had a litter in December 1976. In January 1977 she brought the kittens to her previous home N, but some months later she left again, and settled at U. There she lived partly as a feral cat,

although she "begged" regularly at a couple of households nearby. When staying at N her home range was completely included by the range of cats belonging to household M; these cats also used a barn at N as a secondary home. At U there were no other cats. In summer 1977, she had at least one litter at U, of which two kittens were alive in the beginning of 1978.

Female 812 was born in 1974, and imported as a kitten together with a male of same age, to a farm just outside the study area. There she had a litter in 1975. In February 1976 she moved to household B, (Fig. 3A) where no cats lived at that time. She raised a litter there in 1976, of which two females survived. Female 812 moved again in January 1977, and settled at a household close to B. There she had a litter in May 1977, and in September she left again to some unknown place. At least once during autumn she visited household B, where she behaved aggressively towards her daughters, that still lived there.

Female 817 appeared at a house 0.7 km west of Z (Fig. 1) during summer or autumn 1975; her age and origin was unknown. Gradually she got used to the people and at the end of 1976 she behaved as a domestic cat. No other female cats lived there, but feral and transient males visited the place regularly.

Tab. 2. Dispersal in the Revinge cat population in 1974 to 1977.

	Cats which never changed home area and who reached $\geq$ four years of age	Cats disappeared from home area			Immigrated cats who settled in the study area
		Mortality most likely reason	Dispersal likely but not confirmed	Dispersal confirmed	
♀♀	23	12	4	4	4
♂♂	3	10	15	5	14

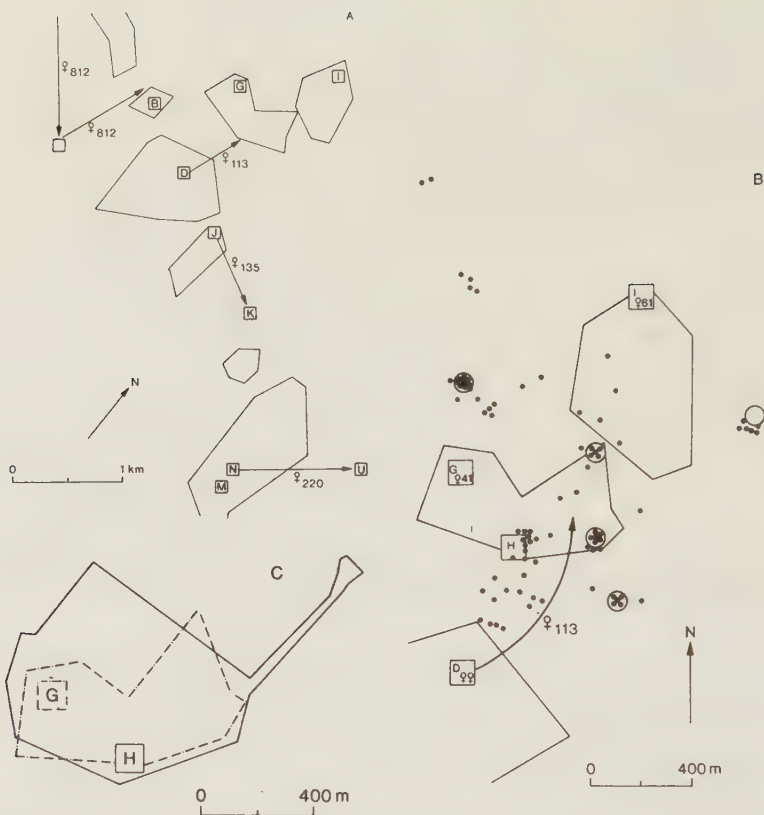


Fig. 3. Dispersal in female cats.

A. Dispersal movements of females in 1975-77 in relation to existing female home ranges.

B. Locations of female 113, radio tracked in autumn 1975, in relation to home ranges of established females in three households. The arrow indicates the principal dispersal movement of female 113. Squares indicates households, circles indicates barns used by cats.

C. Home range of female 113 (solid lines) after settlement in household H in spring 1976. The home range and household of the previous female 41, who died in November 1975, are indicated by broken lines.

Some factors are common for these case studies. All these cats left places with other females, and moved to places without females. The movements occurred when the females were one or two years old. Aggressive behaviour (snarls, attacks, chases) between females was recorded in several cases. The cats moved short distances, usually to the nearest suitable place (Tab. 3).

4.4. Spatial relations between females of the same group

In household D, the home ranges of the adult females overlapped almost completely, especially over a long

period (Fig. 4A). On several occasions two females were seen hunting or moving 30-40 m from each other without being disturbed or taking any notice of each other. However, within the communal home range, the individuals might have had different favourite areas, which was indicated by radio tracking data of four females in household D (Fig. 4B and C).

Also in households Y and Z, little spatial separation occurred between females of the same group (Fig. 5).

In household H, the home range of the female ♀301 was completely within that of her mother ♀113 (Fig. 6). Several encounters, all of them amicable, were observed

Tab. 3. Movement distance of dispersing animals, measured from the original home to the place where the cat first settled. Roman figures indicate first and second phase (see text) of dispersal of female 812.

Females		Males	
Individual no.	Distance, km	Individual no.	Distance, km
113	0.6	123	3.2
135	0.8	78	2.8
812 I	1.1	76	1.2
812 II	1.0	223	2.3
220	1.1	213	2.0
Mean	0.94		2.28

between the two females in different parts of their communal home range.

4.5. Spatial relations between females of different groups

In general there was little or no overlap between home ranges of females belonging to different groups (Fig. 1), even if the households were close enough to make overlap possible, there was none, as with females 41 and 61 (Fig. 7). A similar situation occurred in the same area after these two females had died. Female 113 and her daughter 301 settled in female 41's former range, and female 217 in the previous range of female 61 (Fig. 6). The home ranges of these cats were larger than those of their predecessors. There was a long common bound-

ary and a small area of overlap between the ranges. Encounters between females 113 and 217 were recorded in May 1977, when both cats were radiotracked. They were found a few meters from each other along their common border. As the area was covered by tall grass, I cannot be sure that they were aware of each other. They moved away in different directions after a couple of minutes. Later on this evening female 217 was sitting on a wooden fence, intensively watching female 113, who was approaching along a parallel fence. Female 113 took no notice of female 217, but concentrated on hunting rodents as she slowly walked along the fence. When she was about 30 m from female 217, she turned round, and slowly walked back. Female 217 had been sitting immobile, carefully watching the other

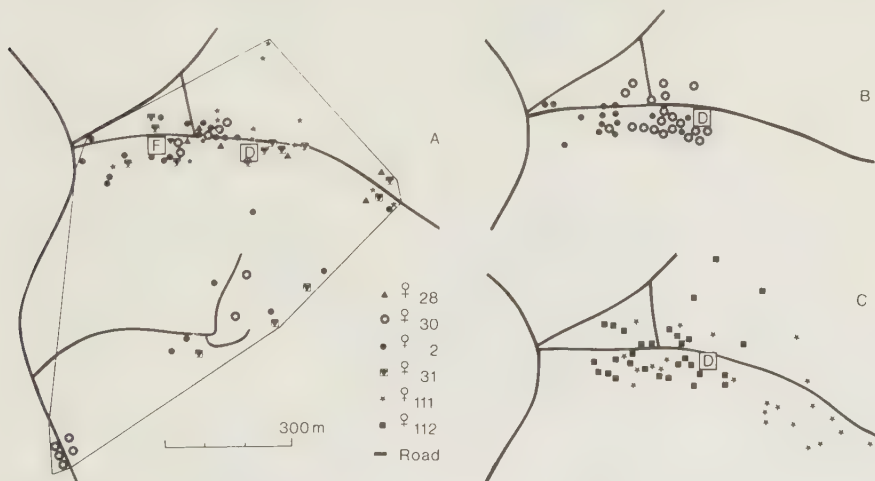


Fig. 4. Spatial relations between females belonging to one household (D)

A. Positions of observations in 1975-77. No positions of female 112, who also lived in the group, were recorded (she was difficult to identify individually from a distance).

B. Locations of two females radio tracked in November 1975.

C. Locations of two females radio tracked in November and December 1977.



Fig. 5. Observations of female cats belonging to households Y and Z in 1973-75 (A) and in 1976-77 (B). The group home ranges are delineated by solid lines.



Fig. 6. Locations of females 113 and 301 of household H and of feral female 217, radio tracked in summer 1977. Home range delineations (solid for 113 + 301, broken for 217) are based on 218 + 95 + 642 radio locations respectively. Locations of cats in home household or inside other buildings are not denoted in the figure, but all such buildings used by cats are marked out.

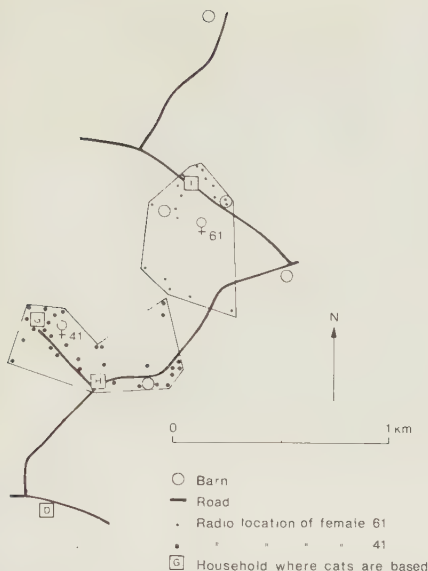


Fig. 7. Locations of females 41 and 61 belonging to different households (G and I), radio tracked in autumn 1975 (♀ 41 16 Sept – 11 Oct, ♀ 61 29 Oct – 11 Nov). The home ranges are delineated by solid lines.

cat. As soon as female 113 turned, female 217 moved towards the center of her range.

Three households (C, E and F) with female cats occurred within the home range of the D female group (Fig. 1). The cats belonging to these households were

rarely observed outside their home sites, so it was impossible to outline their ranges. In this respect they behaved differently to the cats of household D (Tab. 4). The cats of household D might have influenced their behaviour. The owner of the cats in household F reported, that the foreign cats chased his cats and took their places at the food cans.

A similar situation might have existed in the case of female groups T, U, and V. The cats at U, whose primary home was squeezed in between the home ranges of the T and V cats, were observed only once outside their home yard.

4.6. Distribution of males

The distribution of male cats was more complex and dynamic than that of females. First a brief summary of some typical features of male spacing will be given:

(1) A small number of feral males occurred as residents in the area. They were evenly distributed, and usually had large (2–4 km across), partly overlapping, home ranges (Fig. 8). Several households with both domestic females and domestic male cats were included in most of these ranges. In most cases the latter seemed to be subdominant to the local feral male.

(2) Domestic adult males (>1 yr old) occurred in several households. They had larger home ranges than the females, but usually smaller than the feral males (Fig. 9). Domestic males occurring in the same household had a tendency to separate spatially (Fig. 9). Most domestic males were subdominant to the local feral male(s). Fights between domestic and feral males were frequent, usually ending with the domestic male being beaten or chased. Fights or other antagonistic behaviour also were observed between domestic males of the same or neighbouring households.

(3) All domestic males disappeared from their households before they were four years old (Tab. 1). Dispersal was definitely confirmed in only a few cases, but that

Tab. 4. Number of field observations of different female cats living within the communal home range of cats in household D. "Years present in the area" are counted from October 1973, or, for cat born 1973 or later, from 1 January the year after the cat was born, to the date when the cat died or disappeared.

Household	Cat no.	Year of birth	Tot. no. observations	Years present in the area	No. observation per year
D	1	72	4	0.5	8.0
D	2	66	25	4.2	5.9
D	29	66	4	0.7	5.7
D	111	74	12	3.0	4.0
D	31	68	14	4.2	3.3
D	30	68	10	3.0	2.6
D	28	64	7	3.0	2.3
E	24	73	1	0.5	2.0
F	27	73	4	2.4	1.7
F	25	67	2	1.8	1.1
E	109	74	2	3.0	0.7
C	32	66	2	4.2	0.5

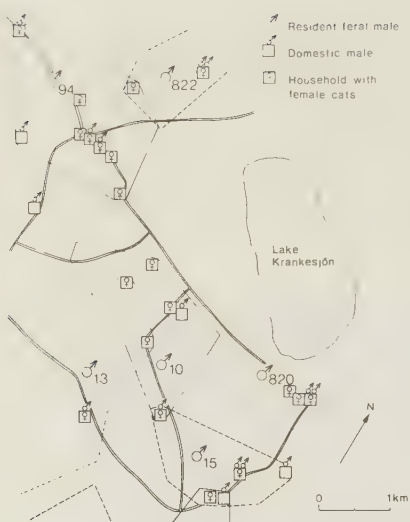


Fig. 8. Home ranges of resident feral males in the Revinge area in spring 1975. The delineations of the home ranges are based on visual observations and trapping data. Households with females and domestic males are marked out.

it occurs more often in males than in females is indicated by the fact that the overwhelming majority of *immigrating* cats are males (Tab. 2). Dispersing males moved longer distances than females (Tab. 3). They settled in areas where no established dominant male occurred, or in marginal parts of dominant males' home ranges. In two cases, domestic males managed to establish a dominant position in their original home areas, and stayed there. In both cases this happened after a previously resident feral male had left the area.

(4) When a resident feral male died, or disappeared from his home range, this was soon occupied by a new male, usually an immigrating feral male.

(5) Transient males of unknown origin were recorded at all times of the year.

To exemplify the dynamics in male distribution, a detailed record of events over two years in the southern part of the study area will be given:

In March 1975, four feral males were established there (Fig. 10A), and in seven households ten adult domestic males occurred. The ferals had large home ranges and seemed to be socially dominant. In frequently occurring fights or clashes between feral and domestic males the former were always superior. In summer 1975, two feral males (No. 13 and 15)

disappeared for unknown reasons. Male 13's former range was split between a new immigrating feral male, 819, and domestic male 85 (Fig. 10B). Six of the other nine domestic males died or left home during the summer of 1975. Male 128 was killed on a road, the fate of males 98 and 124 is unknown, and the other three emigrated. Male 123 was seen on several occasions, west of his original home during summer, and then in autumn 1975 he settled temporarily in the northern part of the newly established male 819's range (Fig. 10B). In February and March 1976, he was involved in fights with a local domestic male (233), was defeated and left the area in March. One occasional observation of him near household V in summer 1977 indicated that he had failed to settle and still lived as a transient animal.

The halfbrothers, males 76 and 78, of household V (Fig. 10A) moved in opposite directions, male 76 to the north out of the study area, and male 78 southward, where he settled in male 15's former range (Fig. 10B). There he established a small home range during the winter 1975–76. In spring he returned to his native home area, after the local dominant feral male 820 had left this area (see below and Fig. 10C). Here he settled during the summer of 1976, although he initially made short visits to his former range. Although he then lived around his original/natal household, he behaved more like a feral male being reserved towards his former owners and was rarely seen at home. He harassed the younger adult domestic male (234) in that household, until this male disappeared in the autumn of that year.



Fig. 9. Home ranges of three domestic male cats (229, 302 and 303) and one feral male (837). Males 302 and 303 were litter mates and belonged to household H, male 229 belonged to household E. The delineations of the home ranges are based on radio tracking during 10 Oct – 20 Nov 1977 (837), 20 Aug – 20 Nov 1977 (302), 20 Aug – 1 Dec 1977 (303) and 22 Nov – 15 Dec 1977 (229).

4.7. Male – female relations

Little spatial interference between males and females was observed. The few cases of antagonistic behaviour recorded between male and female, concerned adult females and adult domestic males of the same group. Sometimes a mother and her son were engaged in such clashes, and female aggression increased before parturition. Usually such clashes were initiated by the female, who hissed or snarled at the male and sometimes attacked. The male reaction usually was avoidance or escape.

5. Discussion

5.1. Proximate factors behind spacing, and the question of territoriality

The most important environmental factors determining the distribution of the cats in this study were the households, on which especially the females heavily depended, because they required much food while breeding. The household at which a cat was at home, was the central point determining the position of the home range. Other factors, like prey density, access to refuge places, sunning spots and places appropriate for breeding, might be decisive for the form and size of the home range, once the location was dictated by the home/household.

Interference or aggressive behaviour between females played a role in dispersal of females, and in determining the forms and sizes of home ranges of neighbouring female groups. The home ranges of groups Y and Z, for example, were placed across the main road going through the area, (Fig. 5) although usually ranges were stretched out along the roads, which the cats used for travelling (Fig. 1). When households containing different female groups were situated very close together a dominance system seemed to evolve.

Male cats, taking no part in raising offspring, were not so dependent on human households for food or cover. Their distribution seemed to be more influenced by conspecifics. The most striking feature of male distribution was that a few males had large and evenly distributed home ranges that together covered most of the area. Was this distribution of male cats an effect of territorial behaviour? Territoriality has been defined by e.g. Howard (1920), Noble (1938), Fisler (1969), Brown and Orians (1970) and Wilson (1975). Wilson's definition summarizes the main points of the concept: "an area occupied more or less exclusively by an animal or a group of animals by means of repulsion through overt defense or advertisement". Resident dominant male cats in this study might fulfill this definition of territoriality. Their home ranges were "more or less exclusive". Whether this was because of repulsion of other males is not completely clear. I never observed territorial dispute between two neighbouring dominant

males. However, dominant males often fought with younger domestic males, and this might have been an act of territory defense. Domestic males got involved in such fights when at different ages, which might reflect a difference in rate of development of challenging behaviour. Age variation between different young males being driven away by territorial males was observed in lion (Schaller 1972) and in roedeer (Strandgaard 1972). Leyhausen (1965) did not regard fights between male cats as primarily territorial disputes. The male cats he studied used an area in common and a hierarchy existed among them. Young males might establish a place in the hierarchy after some initial fighting, that could stretch out for long periods, but after the social position was established, there was little fighting. The social system of male cats in the population I studied was not purely hierarchial. The male cats did not stay in the area where they were born, although their home household offered advantages in form of shelter and a secure food source. Instead almost all of them left their homes sooner or later, and most dominant males were feral, and were not raised in the area where they were resident. In two cases I observed a male cat establish dominance in his original home area. This happened after a former dominant male had left the area at a time when the domestic male had gained enough strength and experience to prevent a newcomer from establishing dominance in this area. The different systems, i.e. territorial and hierarchial, might be due to variations in population density. The cats studied by Leyhausen were either caged animals or urban populations where density was high. The density in my population was extremely low. It might be that at this low level, territoriality could develop, but at higher densities this might change into a dominance order system. This also conforms with the idea of Leyhausen (1965) of "dualism" in many species between "relative" and "absolute hierarchy". The observations of female groups in this study also conforms with such a variation in social system.

Mammals have limited mobility, so their territory defence must rely largely on other means than direct attacks on intruding strangers, e.g. vocal announcement and scent marking. Urine marking was frequent among cats in this study (Liberg unpubl.). Dominant males marked four times as frequently as females and subdominant males. Also, their marking was most frequent in spring, then gradually decreased to reach a minimum in late autumn. This seasonal difference in marking frequency was not observed in females. Also defecation seemed to have a signal function. It has been thought that domestic cats always cover their faeces, as opposed to European wild cats (Lockie 1966). This was the case for all defecations I saw in the cats' home yards or gardens, but 55% of the defecations I observed in the field were left fully exposed. This conforms with the frequency of uncovered faeces in bobcat (Bailey 1974). Pole-clawing and cheek-rubbing were also observed. Even if these different kinds of marking behaviour do

not in itself imply territoriality, they could well have served as territory demarcations, as well as filled other functions.

Some evidence in this study points to territoriality as a cause for spacing and dispersal, both in males, and females. But the picture is somewhat contradictory, and more data is needed, before a more firm conclusion could be drawn.

5. 2. Dispersal

Dispersal has been defined as the movement of an animal from its point of origin to the place where it reproduces, or would have reproduced if it had survived and found a mate (Howard 1960). Dispersal has been reported for a large number of carnivores (Ewer 1973). Typically males disperse further than females, as was also found in this study. The difference in tendency of dispersal in males and females was associated with the different social systems of the two sexes. Howard (1960) distinguishes between two kinds of dispersal; innate and environmental. Caughley (1977) develops this thought further, saying that innate dispersal produces a non-directional movement, while environmental dispersal is less random. Innate dispersal is often longer than the average radius of a home range, whereas environmental dispersal more commonly entails a short journey. In this sense, the dispersal of female cats, in this study is environmental. They moved a short distance, and often settled just outside the native home range, if there was a vacant convenient place. A special type of dispersal was the "seeding out" of kittens recorded for two females. Female 82 dropped one kitten at a vacant household within her home range, and then returned herself to her own home. Female 812 moved from place to place, staying at each household until the offspring reached independence. In three years she dropped three litters at three different places. The adaptive value of such a behaviour must be high, as long as there are empty households around willing to accept these kittens. Factors that apparently caused females to emigrate were crowding and aggression from group mates.

Dispersal in males was a much more general phenomenon than in females. The males left their native area 1-3 yr old. The same age was reported for dispersal of young male lions (Schaller 1972). Those cases, where the movement of the dispersing tomcat was known, point to a directional movement, induced by environmental conditions, i.e. the aggression of a dominant male, towards an area where no such male was present. In lions, aggression from older females also contributed to driving young males away from the pride (Schaller 1972). Occasional observations in this study indicates that this could also occur in housecats, but it certainly was not a general phenomenon.

5.3. Ultimate factors behind spacing

For an exclusively carnivorous predator, living on evenly distributed small prey caught with the aid of cryptic behaviour, exclusive hunting areas should be advantageous (Kleimann and Eisenberg 1973, Ewer 1973). This is the case for the original forms of the house cat, the African wild cat, *Felis lybica* Forster, and the European wild cat *F. silvestris* Schreber.

When domestication of the cat began 3000-4000 yr ago (Ewer 1973), the adaptive value of a solitary life probably decreased radically. At human settlements, where food and cover was provisioned, the survival rate of the cat offspring leaving the settlement was probably lower than the survival of cats remaining with their mother. Tolerance of a female towards her offspring after they had reached maturity, improved the propagation of her own genes. The tolerance should theoretically be limited to kin, and decrease with increasing distance in relationship. On this hypothesis the advantage of staying in the group where the cat was born, would decrease with increasing group size, although this might be moderated by how prepared the "owners" were to increase the food provision in proportion to the numerical increase in the cat group. Breeding success in big groups of house cats is low compared with small groups (Liberg unpubl.), probably as an effect of increased competition for food, as well as other stress factors, like aggression (Leyhausen 1965).

The adaptive value of a female's tolerance towards her adult sons would be less than that of her tolerance towards her daughters. For a mother cat the advantage of increased survival of her sons, if allowed to stay with her, would be reduced by the risk for inbreeding. Also, her genes would spread over a wider area if her sons dispersed, and so came in contact with a larger number of females.

Between adult males, the intrasexual tolerance was shown to be low. One might wonder why not bonds like those between pride males in lion (Schaller 1972), do exist also in the domestic cat. It could be argued that two or three cooperating males would have benefitted from a communal defence of their exclusive access to a large female group. The reason why this has not evolved might be, that the domestic cat lacks an important prerequisite, the cooperative hunt. Lion and the domestic cat social system probably has gone through a parallel evolution, from a solitary way of life to group living (Kleimann and Eisenberg 1973, Leyhausen 1965). Both species have responded to a new environment, where a new way of attaining food might have been the most important factor. For cats it was the availability of a concentrated and predictable source of food (the human settlement), while the lion adapted to large prey on open plains which strongly favoured communal hunting. Kleimann and Eisenberg (1973) considered that the group bonds in lion were based on increased tolerance between closely related females. As already discussed,

this probably also is the case in the domestic cat. But in lion, there also evolved longlasting bonds between males (Schaller 1972, Bertram 1976). One might guess that even if pride males at an earlier stage in evolution held their positions alone, the advantage of cooperative hunting might have kept at least some brothers or litter mates together after they had been driven away from their natal pride. For such a cooperating couple, evicting a lone male from his pride possession is simple (Schaller 1972, Bygott et al. 1979), and once this behaviour was introduced, nothing could stop it from spreading through the population. But in domestic cats, cooperative hunting is of no obvious advantage (it is probably rather the opposite). Therefore there seems to be no mechanism through which cooperation in defending access to females could evolve.

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FOOD HABITS AND PREY IMPACT BY A RURAL DOMESTIC

CAT POPULATION IN SOUTHERN SWEDEN

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CAT PREDATION

ABSTRACT

Natural prey of domestic cats in the Revinge area, S. Sweden, was studied during 1974-79, and related to prey availability. Of 1397 scats, 992 contained remains of vertebrate prey. Mammal prey predominated, both in frequency of occurrence and in weight. The most important prey was rabbit (*Oryctolagus cuniculus*), especially during summer, when rabbit kittens were available. During autumn and winter the importance of rodents, especially *Microtus agrestis* increased. Water voles *Arvicola terrestris* were usually taken in late spring, when both smaller rodents and rabbits were in short supply. Remains of birds occurred in 7,6 % of the scats, but made up only 2,5 % of the prey diet by weight. There was no significant difference in prey selection between house based cats and feral cats, except in autumn, when feral cats took more rabbits. During a spell of severe winter weather in 1977, rabbit intake increased heavily, probably due to the weakened condition of the rabbits. After this winter, the rabbit population declined, and consequently so did the rabbit intake by cats, while small rodents, especially *Arvicola terrestris*, partly compensated for the decrease of rabbits.

Cat predation on *Microtus* accounted for about 18 % of the total annual predation. The latter equalled the estimated annual production of *Microtus*.

INTRODUCTION

Domestic cats are important predators in almost all parts of the world inhabited by humans. Due to this semi-domesticated status, they can often avoid any regulating feed back from the abundance of their prey. Because cats also have been introduced to many places, where prey population have no experience with carnivores, they often are regarded as pests, either by conservationists (Derenne 1976, George 1974) or by human hunters, who see them as competitors (Pielowski 1976). There have been a large number of investigations of cat predatory habits, most of them concerning the relative importance of different prey (see review in Fitzgerald et al. 1979). Microtines and rabbits have been shown to be the most important cat prey wherever they coexist with cats (e.g. Heidemann et al. 1970, Goldschmidt-Rothschild 1976, Jones 1977). Very few studies have collected data that can be used for analysis of the impact on prey populations (Fitzgerald et al. 1979) although many have tried to judge such effects on the basis of their qualitative data (e.g. George 1974, Jones 1977).

Most studies have dealt either with purely feral populations (Hubbs 1951, Jones 1977, Coman and Brunner 1972, Fitzgerald et al. 1979) or with mixed population of house-cats and feral cats, where division between the two fragments of the populations was not possible (Pielowski 1976, Heidemann 1973) or was based on

very crude criteria.

The main purpose of the present study was to measure cat predation in quantitative terms, and put this in relation to prey density and production. Other aspects studied were the seasonal and interannual variations in cat predation in relation to shifts in prey abundance and availability, and also to determine possible differences between house-based and feral cats in their predation pattern and impact.

The study was performed within the context of a general predator-prey study in the Revinge Area in Southern Sweden from 1974 to 1979 (Erlinge et al. in press).

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STUDY AREA

THE HABITATS

The Revinge area (4500 ha) in the southernmost part of the Scandinavian peninsula (55° 42' N, 13° 25' E) belonged originally to the palearctic deciduous forest biome. The Revinge area was previously agricultural land, but since 1965 it has been used for military training. About 40 % of the area is Dactylus glomerata grasslands on mineral soils that are grazed by cattle. Twenty per cent of the area is dry, grassy Corynephorus heath and another 20 % is either dry deciduous forest or brush, or pine plantations. The remaining 20 % consists of wet meadows and marshes on peat soil partly overgrown with willow Salix spp., birch Betula spp. and alder Alnus glutinosa. In the center of the area, there is a small (300 ha) shallow lake called Krankesjön.

Most of the data in this study were collected in the southern half of the area, hereafter called the "intensively studied cat area". Estimates on the total number of prey animals taken by cats, and the discussion on impact by predation refer to the whole area (Fig. 1).

THE CAT POPULATION

Methods used to determine size and structure of the cat population are given in Liberg (1980) and in von Schantz and Liberg (in press). There were no long term variations in cat numbers during the study period, and the number fluctuated between 84 and 121 in the whole study area. Kittens younger than 4 months were not included in this figure because their prey consumption was negligible and virtually all females in the area were house-cats, feeding their young natural prey to a very small extent before that age.

The term "cat-years", is a measure of cat occurrence. When it is referred to concerning a household, it means the sum of all years each cat has been in that household for the period concerned. E.g. if it is said that household A had six cat-years in the period 1974-76, it could mean that two cats had lived there all three years, or that 4 cats had lived there one year each, and one cat had been there two years, or some other combination.

Cats that had a regular contact with one or several households where they were regularly fed by humans are here termed house-cats. Cats without such contacts are called feral. Besides these categories, non-resident cats occasionally occurred in the area. These are called transients and when concerning diet classified together with the ferals. Most of the cats in the area were house-cats; the number of feral cats (all males) fluctuated between 15 and 23.

PREY POPULATIONS

Information on important prey populations of the cats in the Revinge area was available. Among small rodents, the field vole Microtus agrestis L. is the most abundant species. The woodmouse Apodemus sylvaticus L. and the watervole Arvicola terrestris L. occur in lower numbers than field voles. The bank vole Clethrionomys glareolus L. and the greater woodmouse Apodemus flavicollis

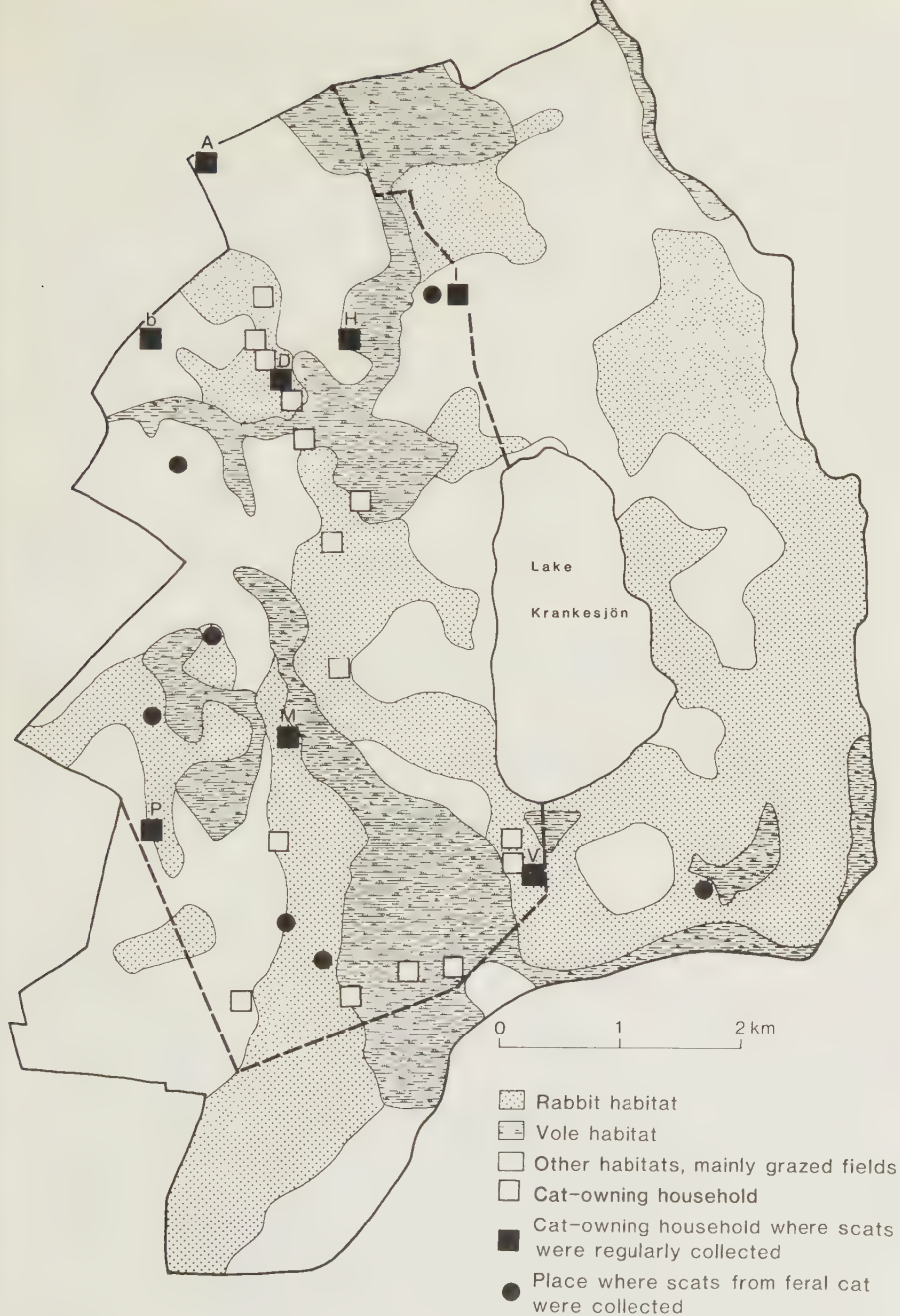


Fig. 1. Study area, with distribution of important prey habitats, cat-owning households and scat collecting places. The extent of the "intensive cat study area" is indicated.

L. occurred in smaller numbers. The small rodents did not show any significant interannual differences in numbers. Instead their dynamics were characterized by low density in spring - early summer and with a peak density in autumn each year (L. Hansson 1971, unpubl.).

Breeding habitats for Microtus and Arvicola are primarily in the wet meadows and the open parts of the marshes (Fig. 1). From these habitats Microtus disperse into wider areas in late summer and autumn. The next spring field voles are again confined to the moist areas. Arvicola moves in the autumn from wet areas to higher dry ground, where they spend the winter in underground tunnel-systems. In April-May they move to the breeding grounds in the marsh habitats (Jeppsson, pers.comm.).

A. sylvaticus is most numerous in non-grazed fields on mineral soil. Clethrionomys and A. flavicollis primarily occur in woodlands.

In terms of biomass, European wild rabbit Oryctolagus cuniculus L. is the most important prey species in the Revinge area. Rabbit colonies were always on dry ground, often in the sandy grass heath. The density was high in areas adjacent to wet meadows that provided luxuriant grazing (Fig. 1). Rabbits were censused by calculating average number of rabbits per warren by means of a mark-recapture programme, and then counting the number of active warrens in the area (Jansson pers.comm.). A second census method used a nocturnal sample plot count with the aid of a spotlight (von Schantz and Liberg, in press). During the late sixties and early seventies, the rabbit population increased steadily from very low numbers caused by the introduction of myxomatosis into Sweden in 1961-62. In 1974-76 the population was still increasing, but in the severe winter 1976-77, the mortality was very high and the number declined. The population continued to decline in the following years, and in 1980 it reached a level about ten per cent of its 1976 density (Fig. 2).

Small game in the area are brown hare Lepus europeus L. and the pheasant Phasianus colchicus. A few pairs of partridge Perdix perdix were observed in 1974-76, but they disappeared after the winter of 1976-77. The populations of hare and pheasant were declining slowly in 1974-76 (Frylestam 1979, Göransson 1980) while later this decline became accelerated, especially in pheasant (Göransson pers.comm.).

Starling Sturnus vulgaris L. and skylark Alauda arvensis L. are the most common passerine birds in summer, while great tit Parus major L. dominate in winter (Karlsson pers.comm.).

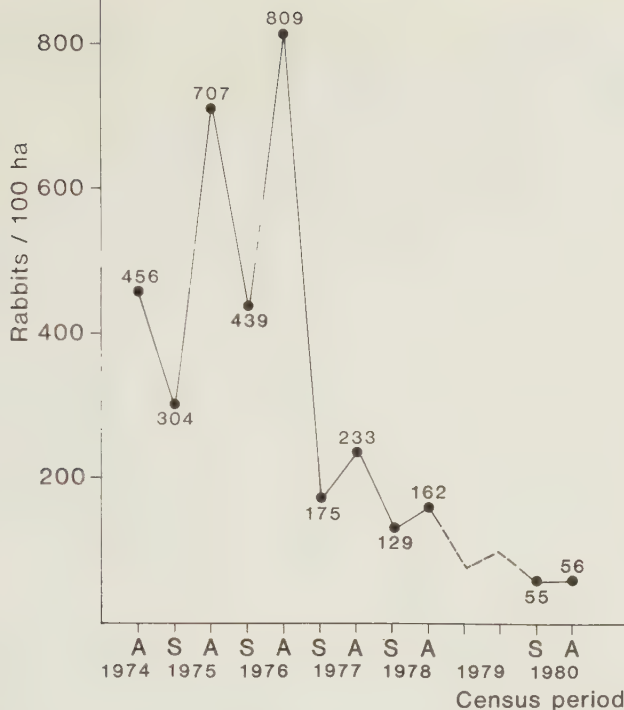


Fig. 2. The dynamics of the rabbit population in the Revinge area in 1974-80. The dashed line indicates an assumed trend in 1979, when no data were obtained. Data are based on night-counts in sample plots (v. Schantz & Liberg, in press) and on warren counts (Jansson, pers.comm.). See text for further explanation.

METHODS

SCAT COLLECTION

Cat predation data in this study are based mainly on faeces analysis. Scats were collected in gardens and outbuildings of cat-owning households, and on tracks and other places where cats were known to travel. Scats found on places regularly used by one or several feral cats, but where house-cats did not regularly occur, were assigned to feral cats (Fig. 1). This way of differentiating scats from feral and house-cats is not completely accurate but the error is probably not large. A total of 1397 scats were collected, 1199 from house-cats, and 198 from feral cats.

In 1974, scat collection was irregular but from January 1975 to August 1977, most scat collecting places were visited once or twice per month. Collecting of scats was also performed in April-May and Oct-Dec 1978 to follow the effects of the rabbit decline on cat diet. There was a continuous period of snow cover from late December 1978 to the end of March 1979, which is unusual in this area. This prevented cats from burying their scats in the earth, and instead they had to deposit them in the snow. When thawing began in March, the scats were easily found as they appeared on the surface of the melting snow. In this way, many more households were sampled during this period than previously. 90 % of all house-cat scats collected in Dec 1974 - Dec 1976 were taken from eight households (Fig. 1), representing about half of the house-cat population (Tab. 1). The Jan - March 1979 sample allowed a check to determine how representative a smaller sample is. Five of the eight households regularly sampled in 1974-1976 were also present in the 1979 sample. The scats from these five households were compared with scats from eight households, that had not been regularly sampled before. Total prey content per scat was higher for the five households, and the same was true for each of the three prey categories. However, the differences were not large and the proportion of different prey types was the same in both groups (Tab. 2).

TABLE 1

Frequency of cat-years and proportion of scats collected, for eight households sampled regularly for scats in 1974-76.

	Households, where scats were regularly sampled								The rest of households
	D	V	P	M	A	I	b	H	
"cat-years" (%) N = 128	16	10	9	6	5	4	2	1	47
collected scats (%) N = 608	26	22	15	9	2	9	2	4	11

KILL DATA

Collection of feathers and lagomorph skins from cat kills provided complementary data, especially on hare/rabbit and pheasant/

TABLE 2

Comparison of prey content of two subsamples of scats, collected during the winter of 1979. Sample I was taken from five households (D, V, M, P and H). These had been regularly sampled during previous years. Sample II was taken from eight households, that were sampled previously only occasionally, or not at all.

Source of scats	N scats	Total prey (g)	Rodents (g)	Lagomorphs (g)	Birds (g)
Sample I (The five households D, V, P, M and H)	95	118.6	5.1	111.2	2.3
$P = 0.124^1$					
Sample II (8 households that had been sampled very little or not at all in previous years)	117	78.9	3.3	75.2	0.4

¹Students t-test. 210 df. $t = 1.5442$.

total bird ratios, that were difficult to get from the scat analysis. Prey carried home by cats was stored by cat owners and later collected by me. Kill remains were attributed to cats also on the basis of type of place where they were found i.e. barns, yards etc. where cats occurred regularly, and where other predators were not likely to occur.

TREATMENT OF SCATS

A detailed description of scat treatment and analysis is given by Liberg (in press). Scats were oven dried and then cleaned by rinsing under water through a 1.2 mm mesh sieve. Teeth and bones were identified macroscopically, hairs and feathers with the aid of a microscope according to Brunner and Coman (1974). Bird remains were usually not identified closer than to family. The cleaned prey remains were then again oven dried, and the different types were separated and weighed. Further analysis was performed in two different ways. Evaluation by frequency of occurrence of prey items has been used in many previous studies. The results are presented in this form in Appendix 1, to facilitate comparisons with earlier studies. Also this type of data are more amenable for statistical analysis of variation, in the form of chi-square-tests. Frequency of occurrence, however, does not give a true

representation of the different prey categories in carnivore diet. Rare food types are usually overestimated and common food underestimated. This can be overcome by weighing the indigested parts of prey that occur in faeces. But this is not enough since small prey has proportionately larger amounts of undigested remains than large prey. Therefore, correction factors, representing the ratio between amount eaten and amount undigested remains for each prey type, have to be applied (Lockie 1958, Goszczynski 1974). For cat prey, such factors have been determined in an earlier study (Liberg in press b.) and are presented in Table 3. For wild carnivores that live entirely on natural prey and leave a fairly constant proportion of undigested remains, the calculation of absolute amount of different prey types eaten is fairly simple. The prey remain weights which have been adjusted by an appropriate correction factor are used to calculate the proportion of the different prey types in a typical diet. Then the daily food demand of the carnivores is obtained, either from literature or from experiments, and multiplied with the different prey type proportions of the diet, to give an average daily intake of each prey type (Goszczynski 1974, von Schantz 1979). This is not possible for a carnivore like the house-cat, where much of the food consists of subsidiaries from the household, leaving little or no traces in the faeces.

TABLE 3

Bodyweight of prey and correction factors used for estimating consumed prey biomass, and number of prey eaten by cats. For rabbits the different correction factors used during various periods are given in parenthesis. Rodents, birds and juvenile rabbits are average bodyweights. For adult and subadult rabbits, weights given are amount of biomass a cat normally will consume from such animals.

	Bodyweights (g)					Correction factors
	Oct-Feb	Mar-Apr	May-Jun	Jul-Aug	Sep	
Microtus	21	30	30	30	30	39
Apodemus	18	21	21	21	21	39
Clethrionomys	16	21	21	20	20	39
Arvicola	100	115	115	115	115	44
Large birds	600	600	600	600	600	382
Small birds	45	45	45	45	45	211
Rabbits	1260(251)	1260(251)	696(217)	498(206)	956(234)	

Instead further calculations are based on the fact that cats seem to have a rather constant defecation rate (see below). Formula (1) gives the daily intake of prey type 1, in grams (B_1).

$$\frac{\frac{w_1}{N_s}}{f} \cdot C_1 = B_1 \quad (1)$$

where w_1 = total weight of remains of prey type 1 in a scat sample

N_s = number of scats in the sample

f = average daily defecation rate

C_1 = correction factor for prey type 1.

Howard (1957) reported that the average daily defecation frequency of one cat in 15 days was about one, and the same rate was reported by the National Pest Control Association in the US (cited in Fitzgerald et al. 1979). In my study of correction factors for cat prey (Liberg in press b.) I found from 9 cats a mean daily defecation rate of 1.02 (range 0.66-1.35).

Number of individual prey animals taken per day was obtained by dividing B with the average body weight of that prey type.

In Table 3 both body weights and correction factors for prey types occurring in this study, are presented. When determining correction factors, only weight of prey hair or feather were included, bone remains in cat faeces were excluded due to high variation in digestability (Liberg unpubl.). Lagomorphs were treated in a special way. Correction factors and body weights have been determined only for rabbits. In the period May-Sep, cats take a mixture of adult, subadult and juvenile rabbits. When determining correction factors these groups were arbitrarily placed in the following size classes: juveniles 100-500 g ($\bar{x}$ = 300 g), subadults 500-900 g ($\bar{x}$ = 700 g) and adults more than 900 g. The adult body weight of 1260 g in Table 3, is not the live weight of an average rabbit in the Revinge area but the average maximum amount a cat eats of an adult rabbit. This was also the weight that the correction factor for adult rabbits was based on (Liberg, in press, b).

Based on teeth and bones from lagomorph remains in cat faeces, the proportions of each rabbit size class in the cat diet were determined for three summer periods (Tab. 4). The mean correction factor and mean body weight for rabbits eaten by cats in these

periods, were determined on the basis of these ratios.

TABLE 4

Size class frequency of rabbits in cats' diet during summer, based on remains in cat faeces.

	May - June			July - August			September		
	Juv.	Subad.	Adults	Juv.	Subad.	Adults	Juv.	Subad.	Adults
N scats with classified remains	10	3	7	23	8	4	2	2	6
%	50	15	35	66	22	11	20	20	60

Because remains from hares were too few to allow their division into size categories with any accuracy, the same procedure and figures were used as for rabbits. This might cause an underestimate of consumed hare biomass, as hares are larger than rabbits. However, as most hares were taken in summer, it is likely that they were young animals, making the size discrepancy to rabbits smaller.

Birds remains were divided into two size classes; for large birds, 600 g was used as the mean weight per prey individual, which was the average consumable biomass of a pheasant; for small birds, 45 g was used, corresponding to the average weight of a fledged starling.

POOLING OF MATERIAL INTO TIME PERIODS

Of the 1199 scats collected from house-cats, 758 contained vertebrate prey. Based on occurrences of different prey, chi-square tests showed that there were few significant differences between months within and between the two different years of 1975 and 1976 (the pre-decline years of rabbit population). Therefore, data from consecutive months were pooled into food seasons, defined on the basis of prey availability and abundance, and data from the same seasons of the two years were pooled. The period of 1977-79 had a different prey situation, and was treated separately. In all statistical tests, three significance levels ($p < 0.05$,

$p < 0.01$, $p < 0.001$) were used, denoted by *, **, ***, respectively.

RESULTS

DIET AND NATURAL PREY CONSUMPTION OF HOUSE-CATS IN 1974-76

All house-cats were fed by their human owners. In 1975-76 this food made up between 50 and 80 per cent of the total intake. It was lowest in summer (Fig. 3).

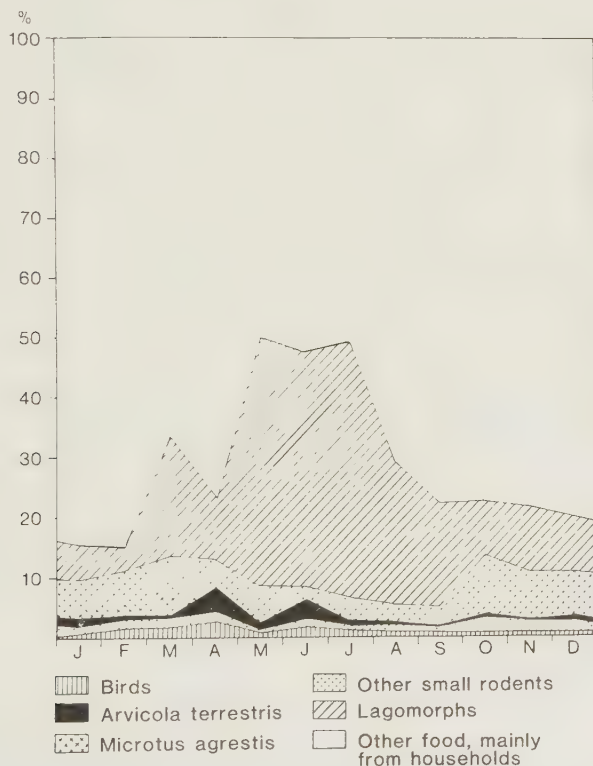


Fig. 3. Percentage of weight, on monthly basis, of food of house-cats in the Revinge area. Based on average figures for 1974-76. N = 608 scats.

Rabbits were the most important prey species in the cats' diet (Fig. 3). The field vole ranked second, while other small rodents were of less importance. Birds occurred in small amounts, and in the scat sample, it was possible to differentiate only between bird orders. Galliformes made up about half the biomass. On the basis of feathers from 89 kill remains, it was possible to determine species of birds in 74 cases. Twenty-one different species were recorded. Starling (Sturnus vulgaris L.) was by far the most common species, making up 46 % of the occurrences. Pheasant (Phasianus colchicus L.) ranked next, with 11 %, while each of the remaining 19 species occurred occasionally. Beside pheasants, wood pigeons (Columba palumbus) and lapwing (Vanellus vanellus) were the only non-passerine species. Most of the starling remains were from juvenile birds.

Small rodents were most important during autumn and winter, while lagomorphs, mainly rabbits, were predominant in summer. Cats switch between these two basic food items in May (Tabl 5). In spring, the water-vole was an important prey. In autumn, the shift from a lagomorph dominated diet to a rodent diet occurred in September (Tab. 5).

TABLE 5

Seasonal differences in the frequency of occurrence of different prey found in scats of house cats. Consecutive seasons in the high rabbit density year of 1975/76 and low rabbit density year of 1977 are compared. Values are Chi-squares. D.f. = 3. Basic data are given in appendix 1.

Tests between consecutive seasons	Jan-Mar	Apr-May	Jun-Sep	Oct-Dec
in 1975/76		7.0(n.s.)	10.6**	66.0***
Tests between consecutive seasons in 1977	47.7***	17.6***	1.1(n.s.)	

The whole scat sample contained very few identified hair tufts of hare (N = 16) so the data from all years were pooled and split up on only winter and summer seasons. The proportion of hares in lagomorphs remains was higher in the scat sample than in the kill sample (Tab. 6A). However, the figures showed the same seasonal trend, with a higher proportion of hares in spring and summer.

Like the hare, pheasant remains in the scat sample were scarce. All occurred during the winter period (Oct-Mar). Kill data gave the same information (Tab. 6B).

TABLE 6

Ratios of hare/rabbits and pheasant/total birds, in cat prey in the Revinge area assessed in two ways.

- A. Recorded number of kills of rabbits and hares, and number of scats where rabbit remains and hare remains were identified.
- B. Number of kills with pheasants and with other bird species, respectively, and number of scats with remains of pheasants and with remains of other bird species.

A. Brown Hare

	Kills			Scats		
	with hares	with rabbits	% hare of all lagomorphs	with hare remains	with rabbit remains	% hare of all identified lagomorphs
Oct-Mar	1	48	2.0	8	111	6.7
Apr-Sep	5	61	7.6	8	37	17.8
All year	6	109	5.2	16	148	9.8

B. Pheasant

	Kills			Scats		
	with pheasant remains	with other bird remains	% pheasant of all	with pheasant remains	with other bird remains	% pheasant of all
Oct-Mar	5	21	19.2	7	45	13.5
Apr-Sep	0	51	0	0	55	0
All year	5	72	6.5	7	100	6.5

CHANGES IN DIET AND PREY CONSUMPTION AFTER 1976

In the severe winter of 1977, the rabbit population declined. Rabbits were abundant all through the winter, and many were in weak condition. Dead, dying, and very weak rabbits were commonly seen. Cats responded strongly to this superabundant and easily available food resource (Fig. 4).

In the previous two years, rodents had been about equally important prey as rabbits in winter, but in 1977 rabbits practically were the sole natural cat prey in this season. In fact house cats lived almost entirely of rabbits, household food made up



Fig. 4. Percentage of weight of prey (household food not included) in house cat diet, on seasonal basis, for the period 1975-79.

less than 20 %. This means that rabbit intake in the winter of 1977 was eight times higher than in the winters of 1975-76. In the winter of 1979, the same weather conditions prevailed, but rabbit abundance was much lower. Then again rabbits were the dominating natural prey in house cat diet, but the absolute intake was only half of that in 1977 (Fig. 5).



Fig. 5. Average daily intake of prey per house cat on a seasonal basis, in 1975-79.

Diets in spring and summer, 1977, did not differ significantly from preceding years. A reduction in rabbit consumption after the population decline was seen in the two samples in 1978. Frequency of prey remains differed significantly when these two periods were compared with the corresponding periods in previous years (Tab. 7). Rabbit consumption was mainly replaced by an increased intake of Microtus and also of Arvicola, especially in autumn. Total prey content in house cat diet was lower in the spring of 1978 compared with corresponding seasons in 1975-76. In autumn 1978 the amount was about the same as in earlier autumns (Fig. 5).

TABLE 7

Interannual differences in frequency of occurrence of different prey. The same seasons of different years are tested against each other. Data from 1975 and 1976 were pooled. Values are Chi-squares. D.f. = 3. N.S. = not significant. Basic data are given in Appendix 1.

	Jan-Mar	Apr-May	Jun-Sep	Oct-Dec
1975/76 against 1977	25.9***	5.9 N.S.	6.4 N.S.	-
" " 1978	-	10.2*	-	10.0*
" " 1979	32.1***	-	-	-
1977 " 1978	-	3.2 N.S.	-	-
" " 1979	4.3 N.S.	-	-	-

The feral cat diet was similar to that of house cats (Appendix 1). There was a tendency toward a higher proportion of lagomorph in most seasons, but in only one period (Oct-Dec 1975/76) was the difference statistically significant (Tab. 8). Total prey intake was much higher in feral cats than in house cats (Figs 5 and 6), as the former were almost entirely dependent on natural prey.

TABLE 8

Differences between house cats and feral cats in frequency of occurrence of different prey found in scats. Values are Chi-squares. D.f. = 2.
N.S. = not significant. Basic data are given in Appendix 1.

	Jan-Mar	Apr-May	Jun-Sep	Oct-Dec
1975/76	1.0 N.S.	4.3 N.S.	2.6 N.S.	6.1*
1977	1.6 N.S.	3.3 N.S.	-	-

However, there was a strong tendency toward a lower total prey intake per individual after the rabbit decline in 1977. In the winter of 1977, feral cats increased their prey consumption, as did the house cats (Figs 5 and 6). In the period following the decline (April 1977 - Februari 1980) the average prey intake was only 179 grams per cat per day, which is below the daily food requirement of a 4.5 kg cat (the average weight of feral cats in the period before 1977).

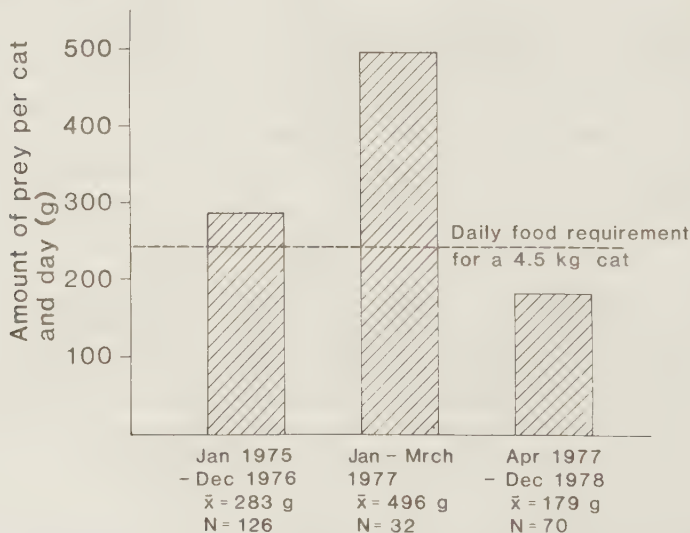


Fig. 6. Average daily intake of prey in feral cats, before, during and after the first winter of the rabbit decline. The level of daily food requirement for a 4.5 cat is indicated. 4.5 kg was the average body weight of a sample of feral cats in the area before 1977.

PREDATION IN RELATION TO PREY ABUNDANCE AND PRODUCTION

The number of prey animals taken was estimated separately for house cats and feral cats, as there was a large difference in the average prey consumption between the two categories. Although the feral cats only constituted 15-20 % of the population, they took about the same amount of prey animals as house cats (Tab. 9).

The number of animals taken by cats in relation to annual production was estimated from pooled data obtained during 1975-1976 (Tab. 9). The most numerous cat prey was Microtus agrestis. The average annual consumption by all cats in 1975/76 was about 30.000 individuals. This corresponds to about 18 % of the estimated annual production of Microtus (Hansson, unpubl.). The most intensive Microtus predation occurred in autumn, when more than half of the annual number was taken, while the lowest number was taken in summer. The annual consumption of Apodemus corresponded to about 24 % of the production of Apodemus sylvaticus, but also A. flavicollis was included in the consumption figure, so the actual impact by cats on A. sylvaticus was lower than estimated. Since there are no complete data on production and densities for Clethrionomys and Arvicola, the impact of cat predation on these populations can not be evaluated.

About 3000 rabbits were taken per year in 1975/76, most of these were kittens taken in summer. This corresponds to less than 4 % of the annual production of rabbits in these years. The total loss of rabbits to cats during the winter, 1977, was considerable, about 2000 animals compared with only 500 in the same season in previous years. However, relative to the total rabbit mortality that winter (estimated at 20.000 to 30.000 individuals, Jansson, pers. comm.) the cat predation was not significant.

IMPACT BY CAT PREDATION ON SMALL GAME

Too few occurrences of hare and pheasant remains were recorded in the scat sample to permit a differentiation between house cats' and feral cats' small game consumption. It was assumed that the hare/rabbit and pheasant/all-bird ratios were the same in both groups. For hares the predation was compared with annual production of hares. As predation of pheasant chickens could not be traced in scat analysis, the number of pheasants taken only applies to adult birds. Therefore, the number of pheasants taken has

TABLE 9

Number of rodents and rabbits taken by housecats and feral cats in different seasons in 1975 and 1976. The figures are means for the two years. The average annual consumption of *M. agrestis*, *A. sylvaticus* and *O. cuniculus* is related to average annual production of these species. The figure of prey consumption for *A. sylvaticus* also includes an unknown number of *A. flavicollis*, which is, however, believed to be small.

	<u>Microtus agrestis</u>		<u>Apodemus sylvaticus</u>		<u>Clethrionomys glareolus</u>		<u>Arvicola terrestris</u>		<u>Oryctolagus cuniculus</u>	
	predation	production	predation	production	predation	production	predation	production	predation	production
Jan-Apr	House cats 4880		820		540		220		150	
	Feral cats 6370		720		660		60		330	
May-Aug	House cats 2510		690		240		170		1000	
	Feral cats 1490		60		80		20		970	
Sep-Dec	House cats 8290		1550		1020		30		250	
	Feral cats 7880		1040		1210		70		460	
All year	House cats 15680		3060		1800		420		1400	
	Feral cats 15740		1820		1950		150		1760	
Total	31420	171,000	4880	20,000	3750		570		3160	90,000
% predation of annual production		18.4 %		24.4 %						3.6 %

been compared, not with total annual production, but with total annual mortality of adult birds. The estimates of annual production of hares and of annual adult mortality in pheasants are means for 1975-76. The cat predation figures are means for the 1975-78 period.

23 % of the hares produced annually were calculated to have been taken by cats (Table 10). Compared with other predators in the area, the cats were responsible for the largest share, while the red fox (*Vulpes vulpes* L.) was next. Considering predation on adult pheasants, the opposite was the case, with fox taking the heaviest toll, and cats responsible for a loss corresponding to about 7 % of total adult mortality.

TABLE 10

Annual cat predation on brown hare in relation to annual production of hares, and on adult pheasants in relation to total annual mortality of adults. Also impacts of other types of predation are given. Fox figures are from von Schantz 1978, other predation figures and figures on production and mortality from Göransson (1980) and Frylestam (1979).

	Brown hare		Pheasant	
	Number	% of annual production	Number	% of total annual adult mortality
Cat predation	370	23	45	7
Red fox predation	260	16	230	37
Other natural predation	110	7	25	4
Human hunting	125	8	145	23
Annual production	1610	100	625	100

The impact of predation on birds other than pheasant, has not been calculated. The bulk of this predation was on young starlings, but compared with the high production of starlings in the area, mortality due to cats was apparently unimportant.

DISCUSSION

DIET

The Revinge cats preyed predominantly on voles and rabbits. This is a pattern shown in many other studies cited in the introduction.

The dramatic switch between rodent hunting in winter and rabbit hunting in summer has not been demonstrated before, although Corbett (1978), reported an increase of rodents in European wild cat diet (F. silvestris) in winter, but rabbits were the predominant prey all through the year. A similar switch between rodent and rabbit diets was described for the common buzzard (*Sylvén pers. comm.*) and for the red fox (von Schantz 1980) in the same area.

As early as March-April cats increased their rabbit intake, although the rabbit population was at its lowest then. But rodents were not a good alternative, since they also are scarce in spring. It is possible that rabbit availability to cats increased, because the condition of rabbits deteriorated in late spring, due to shortage of food at that time. In this period cats also increased predation on water-voles. These animals were practically immune to cat predation during winter, when they live almost entirely in their underground tunnel systems. However, during their spring migration in April and May, down to the wetter areas they are vulnerable to cat predation. Later in summer, they are limited to the wet areas, where cats are reluctant to hunt.

The major shift to rabbits in the cat diet occurs in May, when the first rabbit kittens emerge from the warrens. The rabbit kittens are much more vulnerable to cat predation than are adult rabbits. The most common and efficient hunting technique of the cats, preying on rabbit kittens, was to wait in ambush at the entrances of the rabbit warrens. During midsummer, with a super-abundant supply of juvenile rabbits, the cats took very few adult rabbits. Maximum density in the rabbit population is not reached until August-September and this is the time when cats already are decreasing their rabbit predation. This indicates that it is not absolute density of rabbits that influences the cat population, but rather rabbit availability, in this case the occurrence of juvenile rabbits. In the winters of 1977 and 1979, the adult rabbit availability increased due to the weak conditions of many of the animals. Cats responded very strongly to this especially in 1977 when the increased availability was coupled to an unusually high abundance of rabbits. Some of the rabbits might have been dead before cats started feeding on them. It was shown in another study (Göransson et al. unpubl.), that cats consumed several hundred traffic killed rabbits in this period. Cats also utilized traffic killed rabbits at other times, but this consumption never

constituted a significant portion of the cats' total rabbit consumption.

Birds and small game were not important prey for the cats. An earlier study (Liberg, in press a) indicated that cats spend very little time searching for these types of prey, and they mostly are taken on "passing by", when the cats actually are out for rabbits or rodents. This agrees with most cat predation studies in similar areas (Heidemann et al. 1970, Pielowski 1976, Goldschmidt-Rothschild 1976, Eberhardt 1954). In only two studies were birds reported to have made up the bulk of cats' prey. Both were on islands where there was very little alternative prey, namely Helgoland in the Nordic Sea (Heidemann et al. 1970) and Kergulen in the southern Indian Ocean (Derenne 1976). Hubbs (1951) also found a large proportion of birds in cat diet, although not more than 20 % of all prey items, but he was working with an almost completely feral cat population, living in an area with a high abundance of pheasants and ducks.

Studies that have reported large proportions of murids in cat diet, have usually been performed in parts of the world where Old World rats (Rattus spp.) and house mice (Mus musculus L.) have been introduced and developed into pests in the field (Hubbs 1951, Coman et al. 1972, Fitzgerald et al. 1979). In the Revinge area, rats are rare, and house mice are virtually nonexistent, which probably explains the low occurrence of these species in the cat diet in this area.

No other study has reported the importance of natural prey in relation to "domestic food" for house cats. It is, therefore, not known whether the present cat population is typical for cat populations in temperate agricultural areas in this aspect. It is noticeable that in summer the house based cats actually obtained half their food from their own hunting activities. Maybe such a high component of natural prey in cat diet is only achieved in areas with rabbits or equivalent prey. Still more remarkable was the house cat performance in the rabbit "crash winter" in 1977, when they obviously almost completely stopped eating "at home". However, in other periods, e.g. in April-May 1978, house cats were very dependent on their "owners", when both abundance and availability of rabbits were low, and also rodents were at their lowest annual level.

Casual observations indicate that there are great variations between different cats and also between different households,

concerning the ratio between domestic food and prey in the diet. However, no systematic data on such variations were collected.

The only consistent difference of feral cats' diet from that of house cats was a tendency of feral cats to take more rabbits. In a time budget study of cat hunting in the same area (Liberg in press a.), there were indications that rabbit hunting was more profitable than small rodent hunting. This could partially explain why feral cats, that are dependent on their own hunting, would take a large proportion of rabbits. House cats do not have the same pressure to develop an optimal hunting strategy. Still stronger evidence for the importance of rabbits to feral cats is the fact that their total natural prey intake not only was reduced, when the rabbit population declined, but actually went down below the cats' maintenance level (after a short abundance period during the rabbit "crash" winter in 1977, when feral cats gorged themselves).

Whether feral cats actually starved after the winter of 1977, or whether they found some other food source that did not leave traces in their faeces, like garbage or food from house cat food bins, is unknown. Probably both occurred. The average body weight of feral cats was reduced from 4.5 kg before autumn 1977, to 4.0 kg after that time (Liberg unpubl.). This might indicate, that at least some feral cats had a lower energy intake after 1977. The diet of a Scottish wild cat population (F. silvestris), living in an area with a choice of both small rodents and rabbits, also was dominated by rabbits, and it was shown, that cats could not establish themselves permanently in valleys where rabbits were absent (Corbett 1979).

IMPACT OF CAT PREDATION ON PREY POPULATION

Errington (1946, 1956) stated that vertebrate predators only take a "doomed surplus" of the prey populations, and, therefore, are of little significance in regulating prey abundance. Recent work has opposed this theory. Several field studies indicate that predation has an influence on the dynamics of prey populations (Pearsson 1966 and 1971, Ryszkowski et al. 1973, Keith 1977) and some authors also claim that predation can have a limiting effect on the numbers of prey (Mech 1966, Pils et al. 1978). Other authors have been hesitant to evaluate the effects of predation (Schaller 1972, Kruuk 1972).

Theoretical work has dealt mainly with two- or three species systems (Tanner 1975, Hassell 1976, Roughgarden 1979). However, most predator-prey systems are more complicated, and few models have examined under which conditions one would expect predation to keep a prey population under the carrying capacity of the environment. Davis (1955) pointed out the importance of a food buffer for a predator, expected to have a limiting effect on a particular prey population. Such a buffer could either be another prey species occurring in excess, or some other type of food. The buffer makes the predator less dependent of the density of the affected prey population, and high predation pressure can be maintained on this prey, even when it becomes low in numbers. Cats, provisioned with food by humans, is an example of this type of predator. Elton (1953) found that farm cats could limit a local rat population on farms up to a distance of 50 m from the farm. Davis (op. cit.) obtained similar results. Whether cats can have the same impact on field living prey, is more questionable, as was already demonstrated in the study by Elton. Rats in corn ricks further away from the farms than 50 m were not affected by cat predation. George (1974) on the other hand, considered cats as very effective vole hunters, causing shortages of winter food for raptors over large areas in USA. Ryszkowski et al. (1973) found that farm cats were one of the most important vole hunting predators in agricultural land in Poland. Their study demonstrated a quick numerical response by cats to increasing numbers of voles (Microtus arvalis). The farms functioned as "cat reservoirs" in years with low vole numbers. When vole numbers increased, the cats spent increasingly more time hunting in the fields, up to ten times more in the peak phase of the cyclic vole population, compared with other times of low density. In spite of this rapid numerical response, that hardly could be performed by natural predators, neither cats alone, nor the total predator guild could prevent the outbreaks of the vole population.

On the other hand, Fitzgerald et al. (1979) showed that feral cats in the Orongorongo Valley in New Zealand were "a major factor determining rat densities". Similar conclusions were drawn for the cats' effect on the feral house mouse population and on the rabbit population. All three prey species were introduced in the area, as were cats. Feral cats that appeared to limit rabbit populations were also reported by Gibb et al. (1969) and Gibb (1973) from N.Zealand pasturelands.

Of the studies mentioned, only Ryszkowski et al. took the impact of the whole predator guild into consideration. In the Revinge area, the effect of predation has been viewed in a community context. All of the most important cat prey species in the area (Microtus, Apodemus spp., Arvicola and Oryctolagus) are also food for a number of other predators, among which red fox and common buzzard Buteo buteo, together with cats are the dominant species, considering total prey biomass taken. Cats alone seem to have a small or negligible effect on most of its prey species, but together with other predators, it has been found to remove almost the total annual production in Microtus agrestis and Apodemus sylvaticus (Erlinge et al. unpubl.). Rabbits, on the other hand, did not seem to be limited by predation, as they increased all through the early seventies. Here the total predator guild removed only about 25 % of the annual production in the years of 1975 and 1976. The decline of the rabbit population in 1977-80, was obviously caused by adverse weather conditions causing food shortage in hard winters. The situation in 1979-80, with a heavily reduced rabbit population, however, could be different. Then it was quite possible that predation might have been limiting the rabbits, or at least causing a delay in population growth recovery. Such a "down-pressing" and "prolonging of the low phase" effect on prey by predators was demonstrated by Pearsson (1968) and Keith (1977) on Microtus californicus and snow-shoe hare, respectively.

The cats' impact on game species is hard to evaluate. A toll of 23 % of the hare production probably has some effect on numbers of hares to be harvested by hunters in autumn. Whether it also effects the level of breeding hares in spring is uncertain. Too little is known about other mortality factors of hares, about the relation between hare populations and its winter food, and about the social system of hares.

For pheasants, where most of predation on adult birds occurs in late winter, it seems more likely that cats might have reduced the breeding population. But it could also be argued that the birds taken by cats probably were in such bad condition, that they would not have survived anyhow (Erringtons "doomed surplus"-theory). It is quite likely that cat predation pressure on small game was higher in 1977-79 than in 1975-76. Cat predation seemed to be the same, but prey populations underwent an accelerating decline.

In other European studies, cat predation on game has been re-

ported to be low (Pielowski 1976, Heidemann 1973, Goldschmidt-Rothschild 1976, Spittler 1978). However, none of these studies was able to demonstrate in absolute figures how the predation loss compares to other types of mortality, or to production of the prey populations.

In the present study, no confidence limits have been given. However, they probably are rather wide. A comparison with a time budget study on hunting cats in the same area in 1974-77 (Liberg, in press, a) offers an opportunity to check the reliability of the predation rate. According to that study, about 58.000 small rodents were taken for the period Sep-Apr each year from 1974-77. This should be compared with the figure of 35.000 from the method presented in this paper.

In a study like this, with so many variables involved, one might be content with this rather poor correspondence. I will, however, discuss two factors which might cause underestimates in the present study.

The first concerns defecation rate. It has been shown that cats on a fluid dominated diet (e.g. milk) often have a chronic diarrhoea, raising daily defecation rate (Panaman, 1981). It is quite possible that many cats in my area, at least periodically had such a diarrhoea. Several scats collected were very loose. This phenomenon tends to put too much emphasis on this type of scat, for instead of representing a whole day's food it may be representing only a part of a day.

The other factor is that most house-cat scats were collected at, or very near, houses. This gives an over-representation of those cats that hunt least, i.e. those that stay at home most of the time. The best hunters spend more time in the field, and are thereby more likely to drop a larger proportion of their scats in the field.

A comparison between a "field-sample" and a "house-sample" of scats, collected in the same periods, also revealed that the field-sample contained about three times as much prey remains as the "house scats".

On the basis of this discussion, one might regard the predation figures presented in this study as minimum figures.

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APPENDIX 1

Occurrences of four prey categories in house cats and feral cats, by four seasons in 1974-76 (pooled) and in some sampling periods in 1977 to 1979.

Small rodents include *Microtus*, *Clethrionomys*, and *Apodemus* spp.

	Small rodents	Arvicola	Lago- morpha	Aves	Σ occurr- ences	N Scats
<u>House cats</u>						
<u>1974-76</u>						
Jan-Mar	45	4	22	9	80	136
Apr-May	42	9	40	5	96	122
Jun-Sep	43	18	90	19	170	201
Oct-Dec	110	5	34	8	147	195
<u>1977</u>						
Jan-Mar	24	1	56	3	84	103
Apr-May	13	9	21	5	48	42
Jun-Aug	29	14	33	6	82	75
<u>1978</u>						
Apr-May	10	5	9	7	31	37
Oct-Dec	44	8	7	2	61	64
<u>1979</u>						
Jan-Mar	18	3	65	8	94	224
<u>Feral cats</u>						
<u>1974-76</u>						
Jan-Mar	50	3	23	6	82	69
Apr-May	21	2	8	0	31	25
Jun-Sep	9	1	10	0	20	16
Oct-Dec	15	1	13	0	29	26
<u>1977</u>						
Jan-Mar	15	0	29	4	48	37
Apr-May	10	0	10	8	28	20
Jun-Aug	3	2	3	0	8	5

HUNTING EFFICIENCY AND PREY IMPACT BY A FREE ROAMING

HOUSE CAT POPULATION¹

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ABSTRACT

Hunting in free roaming house cats, Felis catus L., was studied by visual observations. A total of 104 hours of observations of cat activity in the field was recorded. Cats concentrated on rodent hunting in autumn and spring, while rabbit hunting dominated in summer. Rodents were taken in about five times as short a time as rabbits, but the time input per rodent taken increased from about 40 minutes in autumn, when rodent populations had their highest density, to about 70 minutes in early summer, when rodent populations were at their lowest values. Differences between domestic females and feral male cats in hunting efficiency and prey selection are discussed in terms of social behaviour and optimal foraging. Cat occurrence in the terrain was measured by counts in sample plots during the day and night. Numbers of rodents taken by cats in the whole area per autumn and spring periods were computed. These figures are compared with corresponding figures based on analysis of faeces, and the discrepancy between the estimates from one of the seasons is discussed. It is estimated that cat predation accounts for 20-40 % of the winter loss in Microtus agrestis.

Key words: cat, Felis, feral, house-cats, hunting, predation, prey, rabbit, rodent, time-budget

INTRODUCTION

Free roaming domestic cats Felis catus L. are important predators of small vertebrate prey, especially rodents (Pearsson 1964, Ryszkowski et al. 1973). In a joint study of predator-prey relationships in southern Sweden (Erlinge et al., in press) several aspects of house cat predation were studied. Most data on prey selection and numerical exploitation of prey populations are based on faeces analysis, but here I will report on a study of predatory behaviour of house cats based on visual observations. This method yields information on the time budget of the hunting cats, which then can be used to calculate numerical exploitation of the prey. This can be compared to the corresponding data received from faeces analysis, which is especially valuable since exploitation figures based on either method were impossible to evaluate statistically.

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METHODS

STUDY AREA

The study was performed in the Revinge military training area in southernmost Sweden (55.42 N, 13. 25 E) and was carried out from autumn 1973 through 1977. The area, 45 km², was used for agriculture until 1965. About half of it is now cattle grazed fields, and 20 per cent consists of marshes and wet meadows with tall grasses and herbs and partly overgrown with willow, alder and birch. A quarter of the area is made up of sandy hills partly planted with pine. Small woods of deciduous trees and patches of brush are distributed throughout the area. Rodent populations, where Microtus agrestis L. is the most important species, are concentrated in open wet areas, with lower densities in grass fields. In the sandy hills dense populations of wild rabbits Oryctolagus cuniculus L. are the most important prey of cats. Other potential cat prey in the area are European hare, pheasants and small birds.

The cat population in the area consists mainly of tame house cats and a small fraction of feral male cats. The density of the population was about 3.0 cats per km². The population is described in more detail elsewhere (Liberg, 1980).

OBSERVATIONS OF HUNTING

From October 1973 to June 1975, cats were located in the terrain while slowly driving or walking through the area. When a cat was spotted, notes were taken of identity, position, date, time of day and activity. A cat was followed for as long as possible without disturbing it by making observations with the aid of a pair of ordinary 10x50 binoculars and occasionally with a 20x telescope. Continuous notes were taken of the activities of the cat.

When cats were hunting rodents it was not always possible to see what prey was actually taken because of long distances and tall ground vegetation. However, it was possible to determine whether an attempt had been successful or not. When a cat had caught a rodent, it invariably moved a few meters away from the place of the catch, then laid down and ate. Usually the whole process, beginning from the leap until the cat left the place, took 70 - 110 seconds and never less than 55 seconds. When a leap had failed, the cat always left the place within 35 seconds

after the leap. It was rarely possible to see which species of rodents the cat had caught, and therefore all small rodent species are lumped in one category in this report. Determination of rodent species in the cat diet in this area is made on the basis of faeces analysis, and will be reported elsewhere.

After June 1975, some cats were periodically equipped with radio transmitters, mounted on collars, to facilitate the location of cats, and this also made it easier to keep in contact with the cats even when they intermittently could not be seen. Transmitters were of the same type as described by Tester et al. (1964). A total of 24 different cats, 12 males and 12 females were equipped with transmitters for periods from one week to five months.

IDENTIFICATION OF CAT INDIVIDUALS AND POPULATION DATA

Throughout the study period I had frequent contacts with the households that kept cats to get information on the number of cats and their identity. Most cats were identified by the patterns of their coat colour. Feral cats were trapped so they could be sexed and weighed, and usually they were then marked with collars or earnotches. A thorough knowledge of the size and structure of the cat population was obtained by information from the households, trapping and observations in the field.

MEASUREMENT OF CAT OCCURRENCE IN THE TERRAIN

To get information how many cats were hunting in the area at any given time, counts were made in sampling plots. There were 120 plots distributed over the area, covering a total of 280 ha. Plots were placed in all habitats in about the same proportion as the habitats occurred in the area, except for forests which were underrepresented. Counts were made during two periods each year, one spring period in March-April and one autumn period in November-December. Between eight and ten counts were made in each period, half of them in daylight and half of them in darkness. At night counts were made with the aid of a hand-held spot-light.

RESULTS AND DISCUSSION

PREY SELECTION AND HUNTING SUCCESS

About 3500 hours were spent in the field in search of cats, in trapping and in radio-tracking cats, but as cats have a cryptic behaviour, and, especially in the vegetation period, are hard to spot, only 104 hours of cat activity outside human settlements were recorded. Observations were compiled from 236 different occasions and included 122 different individuals. Most of this time were spent on hunting (96 hr), while other activities included resting, grooming, travelling and social activities like courting and mating.

Two types of prey predominated, small rodents and rabbits (Table 1). Occasionally cats were observed hunting small birds, pheasants and even once an adult hare. In some cases, it was impossible to assign the hunt to a special object. A greater proportion of their time was spent on rodent hunting in autumn and spring than in summer. Rodent populations reach their annual peak at the beginning of autumn, and then decline all through winter to reach their lowest values in May (Hansson 1979). At this time cats switch over to rabbits and also because the rabbit kittens are easily caught when they start to emerge from the warrens in May. From then on there is a good supply of juvenile rabbits through the summer which attracts a good deal of the cats' hunting attention.

A meaningful comparison of hunting efficiency between seasons, and between cat categories could only be determined from data for rodents. Comparing season, the efficiency was highest in autumn, then decreasing in spring and summer which parallels the development of the rodent population density. Although the difference is not statistically significant ($\chi^2 = 1.33$, $df = 1$), there is an indication that feral males were more efficient rodent hunters than females, especially in spring. One reason could be that competition for good hunting ground is stronger between females than between feral males. Most females live in groups of two to eight adult cats in one household, sharing the same hunting grounds (Liberg, 1980). It is therefore quite possible that females deplete their hunting grounds more so than the feral males who roam over wider areas and have access to food patches where no other cats hunt. A comparison of rodent density in two meadows in January 1978 might support this explanation. In one meadow,

TABLE 1

Number of minutes cats were observed hunting different prey types, number of prey items taken, and number of minutes/prey taken.

Season	Category of cats	Females			Domestic males			Feral males			All categories of cats		
		Min.ob- serva- tion	Number prey taken	Min./ prey taken	Min.ob- serva- tion	Number prey taken	Min./ prey taken	Min.ob- serva- tion	Number prey taken	Min./ prey taken	Min.ob- serva- tion	Number prey taken	Min./ prey taken
Jan.-Apr.	Rodents	510	7	73	146	2	73	605	13	47	1261	22	57
	Rabbits	57	-	-	44	1	44	131	-	-	232	1	232
	Others	59			30			-			89		
May -Aug.	Rodents	921	13	71	48	2	24	177	1	177	1161	16	73
	Rabbits	714	2	357	165	1	165	584	1	584	1507	4	377
	Others	38			44			-			82		
Sep.-Dec.	Rodents	591	13	45	49	1	49	556	15	37	1196	32	38
	Rabbits	38	-	-	3	-	-	110	1	110	151	1	151
	Others	56			-			81			137		

1. χ^2 for distribution of rodents taken, over seasons = 5.8, df = 2, p < 0.05.

almost daily exploited by three female cats from a house nearby, 7 small rodents were caught in 90 trap-nights. In another similar meadow more than one kilometer from any cat-holding house, and where only occasionally a feral male cat had been observed hunting, we caught 18 rodents with the same trapping effort ($\chi^2 = 4.7$, 1 df, $P = 0.03$).

In summer, the only season where I recorded more than one successful hunt on rabbits, the cats had to spend about five times longer to catch a rabbit than to catch a rodent.

In this period, most rabbits taken by cats are kittens, with an average weight of 300 g which is ten times the weight of an average rodent. This means, that in the same time that a cat could take 150 g of rodents (five animals) it could take 300 g of rabbits (one average juvenile). In other words, rabbit hunting provides double the rewards as does rodent hunting in summer. Therefore, it is surprising that female cats still spend more time on rodent hunting than on rabbit hunting in this season (Table 1). However, all females in this area are housebased, and not dependent on their hunting, as they are fed by humans. Therefore they do not have to optimize their hunting behaviour (Schoener 1971). Also, female activity periods were usually short, seldom more than two hours, as revealed by telemetry (Liberg unpubl.), probably because many of them had kittens at home to care for. Now, if female cats were not hunting to fill their energy requirements, but to satisfy some kind of innate need for hunting, it would have been more rewarding for them to hunt rodents, as their short activity periods seldom were long enough to make a catch of a rabbit possible. For feral males the situation was just the opposite. They were not restricted in their activity by the responsibility for raising kittens, but they were indeed dependent on their hunting, so for them rabbit hunting would be the optimal strategy. It was also shown that they spent three times as much time on rabbit hunting as on rodents in summer (Table 1). Hunting success, measured as the number of leaps per prey individual taken was higher for rodents than for rabbits. For rodents, cats succeeded in about every second leap, which is the same hunting success that was recorded by Leyhausen and Wolff (1959). For rabbits, the leaps were successful only every fifth time (Table 2). Most of the rodent hunts were made in bogs, meadows and grass fields, while rabbits were hunted predominantly in dry areas, where they had their warrens.

TABLE 2

Number of successful (+) and unsuccessful (-) cat hunting efforts for rodents and rabbits in different habitat types.

	Wet meadows and bogs	Grass fields	Sandy hills	Dry deciduous forests	Coniferous plantations	Road sides	Total						
	+	-	+	-	+	-	+	-					
Rodents	51	46	14	21	5	5	1	1	72	75			
Rabbits	1	-	-	2	2	11	3	2	-	5	-	6	20

TABLE 3

Number of cats counted in sample plots (of open habitat types) in 2 different seasons and divided per day and night.

	Sep - Dec			Jan - Apr				
	Number of counts	Number of cats seen	Cats/ Count	Computed number of cats in total area	Number of counts	Number of cats seen	Cats/ Count	Computed number of cats in total area
Day	12	10	0.83	10.4	14	8	0.57	7.1
Night	15	17	1.13	14.2	19	10	0.53	6.6

Collected data were large enough only for rodents to make calculations of absolute number of prey taken possible. Data collected were average number of prey taken per time unit (Table 1), and average number of cats hunting at any given time in the area. The latter figure was taken from the sample plot counts (Table 3). No counts were made in the summer season because of tall vegetation. Therefore no calculations of rodent numbers taken could be made for that season. The number of hunting cats out in the open, was lower in spring than in autumn, probably because of two factors: 1) in spring cat activity is more directed towards reproductive behaviour such as courting and mating, which usually takes place in the yards and outbuildings of the homes of the females; 2) prey density was lower and weather conditions more adverse in spring than in autumn, both contributing to a lower hunting activity in the tame cats, who constitute the majority of the population. Because hunting was observed only in daylight, no figures on hunting efficiency in darkness could be obtained but was assumed to be the same as in daylight. Because this is an uncertain assumption, the calculation of number of rodents taken per day was split between two twelve hour periods, which approximates the periods of daylight and darkness per day in autumn and spring in this area. Then estimated number of rodents taken in daytime will be a minimum figure, while the total estimate including also night-caught rodents will be more uncertain, and probably indicates a maximum since it is difficult to imagine that rodent hunting could be more efficient in darkness. This is because neither cat hunting behaviour nor rodent escaping behaviour are dependent on light conditions, and also as rodent activity is rather higher in daytime than in nighttime in winter (Bäumler 1975). The number of rodents taken per 12-hours period was calculated according to the formula:

$$N_c \cdot \frac{12 \cdot 60}{m} = N_r$$

where N_c = average number of cats in field at any given time during day and night respectively (Table 3)

m = number of minutes cats spent in field per rodent taken (this is not the same figure as the "min/prey taken" in Table 1; this figure includes all time of all types

of cat activity in field per rodent taken, as I could not always specify what the cats in the sample plots actually were doing)

N_r = total number of rodents taken by cats in the study area per 12-hour period

TABLE 4

Number of rodents taken by the cat population in autumn and spring.

A) Based on time budget studies

	Sep-Dec	Jan-Apr
No rodents taken in daytime (0600-1800)	18.300	7.800
" " " " nighttime (1800-0600)	<u>24.900</u>	<u>7.200</u>
Σ	43.200	15.000

B) Based on faeces analysis (Liberg unpubl.)

Sep-Dec	Jan-Apr
21.100	14.300

The total number of rodents taken by cats in the autumn (Sep.-Dec.) and spring (Jan.-Apr.) season were calculated respectively (Table 4). These estimates were compared with corresponding figures based on faeces analysis (Liberg unpubl.). The high discrepancy between the results of the two methods for autumn (Table 4) could have been caused by an error in the assumption, already discussed, that hunting efficiency concerning rodents is the same during the night as it is for the day. However, for the spring season the estimates of the two different methods are very similar (Table 4). A possible bias in the collection of scats could be, at least partly, responsible for the higher discrepancy in autumn. Tame cats deposit most of their scats around the homes, in the gardens and backyards simply because they spend most of their time there. Consequently the number of scats deposited out in the field is proportional to the amount of time cats spend there. However, there is also a strong variation between different cats in hunting activity. Cats that hunt much, would also be expected to deposit a larger proportion of their scats in the field than cats that are hunting less and stay more at home. It would also be expected that "field-droppings" contain more prey remains than "home-droppings". In autumn cats spent more time in the field (Table 3), therefore there would be a higher proportion of "field-droppings" in that season. But in both seasons I collec-

ted most of the scats around the cats' homes, simply because the "field-scats" were extremely hard to find, and also that they sometimes are difficult to distinguish from fox scats. This means that in my sample, "field-scats" are more underrepresented in autumn than in spring, which also means that amount of prey remains in the scat sample will be underrepresented.

About 80 per cent of the rodents taken by the cats were Microtus agrestis according to the faeces analysis (Liberg 1981). This would mean that between 28000 and 46000 Microtus were taken by the cats in this area during the nonreproductive period (Sept.-Apr.). That corresponds to 20-30 per cent of the total winter loss in the Microtus population (Hansson unpubl.). It is obvious that the cat population alone would not regulate the Microtus population but together with other predatory species in the area, they account for the total winter-loss (Erlinge et al., in ms).

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COURTSHIP BEHAVIOUR AND SEXUAL SELECTION IN THE

DOMESTIC CAT

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Oestrus timing and courtship behaviour in a rural free-ranging domestic cat population were examined and discussed in the context of sexual selection theory. Female cats in the population were seasonally polyoestrus, breeding maximally three times a year. Contrary to prediction from theory, oestrus was found to be synchronized within female groups. In most cases females were courted by several males simultaneously. One was always much closer to the female ("Central Male" = CM) than the others ("Peripheral Males" = PMs). The CM was dominant over the PMs, and performed all copulations. CMs were usually older and larger than PMs, or males that did not at all participate in competitive courtship. Young males were recorded to mate with females of their own kin group, while courting them in absence of other males. Female habit of moving around fastly and frequently during courtship, caused increased competition between males. CM-PM aggressions were more frequent and more serious than PM-PM aggressions. Most conflicts were settled by threat displays, fights were relatively rare. Exchange of CM occurred frequently, most commonly as a result of a CM leaving his position unprovoked, or when a former CM resumed his position after some time's absence.

INTRODUCTION

Domestication probably has had very little effect in the sexual activities of the domestic cat (Felis catus L.). Cats usually are free to roam and establish social relationships with conspecifics in the area, including the freedom to choose sexual partners, as do their wild relatives. Persons living where free-roaming cats occur are well acquainted with the calls and sounds of rituals and fights between cats during the breeding season. Significance of this behaviour in competition for matings, has not been studied. Basic sexual behaviour, such as announcement and inviting behaviour of the female, or behaviour during copulation, have been excellently described by Leyhausen (1979), Scott (1970), Beadle (1975), Hart (1977) and others and will not be further described here.

Instead, this paper tries to identify and evaluate factors, important for mate selection in the domestic cat. To this end I investigated occurrence and synchrony of oestrus, cat behaviour during courtship with emphasis on competitive behaviour of males, and selective behaviour of females. I also gathered data on age and weights of male cats in the area, to assess whether these factors influenced competitive ability. Data on frequency and timing of oestrus were collected from 1974 through 1981. Most observations were made in 1979 and 1980, and to a less extent in 1981.

STUDY AREA AND THE CAT POPULATION

The study was performed in the Revinge area in southern Sweden. The area and its cat population was previously described in Liberg (1980). The behaviour observations were made in the south-west corner of the Revinge area, including 500 ha of mainly open grassland with scattered groves and lines of deciduous trees and bushes, and a few marsh areas. It contains about 20 permanent households, of which cats live in ten. Female cats occur in seven households. When several cats lived in the same household, they were usually closely related to each other (Liberg 1980). The total number of cats in the area varied between 25 and 35. Since the area was used for military training, no dairy or other type of small farms occurred in it, but only one large cattle ranch. There were several partly or completely abandoned farms and other buildings in the area, places much used by cats.

METHODS

Data on occurrence and frequency of oestrus were obtained from the cat owners. Since almost all female cats in the area were tame (two were what might be termed "semi-tame", i.e. they changed household several times, and did not "belong" to any particular person) and mostly were in daily contact with their caretakers, birth dates of litters were usually known. Dates for oestrus periods (which often was more difficult for the owners to observe and define) were then calculated by counting back the average gestation period of 65 days (Prescott 1973, Scott 1970, Jemmet et al. 1977) from the date the female gave birth.

Studies of courtship behaviour were facilitated by equipping male cats with radio transmitters (Tester et al. 1964, Liberg 1980). Thereby their exact position could be determined. Even if only one of a number of male cats that were courting a female, was radio-equipped, this was a large help for the observer to keep in touch with what was going on.

Cats were individually identified on basis of their natural coat colours, or in a few cases with a collar (Liberg 1980). Also the radio transmitters helped in individual identification. All resident cats in the area could be identified from a distance of at least 50 m in the field.

The following factors were always noted during an observation:

1. date and time for the observation, and identity of cats observed,
2. number of minutes a female was under direct observation,
3. positions and movements of all cats in the "courtship area" (see below),
4. each copulation, and copulation attempt,
5. aggressive behaviours,

Also other events judged to be of interest, were noted. In an effort to understand why a male, that leaves the courting area unprovoked, was doing so, such males were followed in some cases to determine their destination.

The following aggressive behaviour were identified:

1. fights,
2. chases,
3. vocal duels (Leyhausen 1979, Beadle 1977),
4. threat displays without, or with slight, vocalization, (Leyhausen 1956),
5. a cat being deterred, without any preceding visible aggression (repulsions)

In each aggressive conflict between two cats, an attempt was made to determine which one was dominant, and which was subordinated. On basis of this, each opponent was allocated either a "victory" score, or a "loss" score. Male cats that left a courtship area within an hour after arriving there, were classified as have performed a "withdrawal" and were also given a "loss" score.

The term "courtship area" is used more in a functional than a geographical sense. A male being in the courtship area, means a male that both is in the vicinity of the female in oestrus, and also is showing interest in her.

Extensive data were obtained from fourteen oestrus periods. More sporadic observations were made at another thirteen periods. No oestrus period was covered completely from start to end. Due to the elusive behaviour of the cats, especially the females, the length of time the cats were under direct observation, was considerably less than the time the observer spent with them. With the aid of the radio-transmitters, it was, however, possible to keep in touch with the cats, even when they were out of sight for hours.

RESULTS

BREEDING SEASON

The main breeding season was between February and July, with a few females in heat in January and August - October (Fig. 1). The one-year-old females usually came on heat later in the year than the older ones (Fig. 2). There were two peaks in the season, the first one in February-March, and the second one in May caused by females coming into their second oestrus. A much lower proportion of the young females, than of the older ones bred twice a year, but there were also a number of the older females that only had one litter in the same year. Few females bred more than twice, and no one more than three times a year.

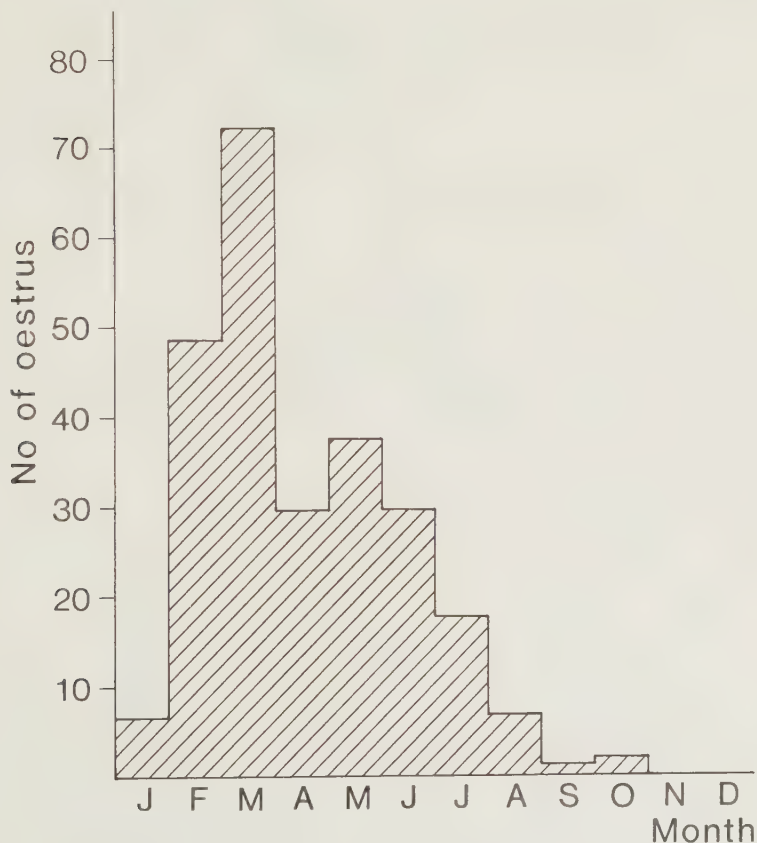


Fig. 1. Annual distribution of oestrus periods in the Revinge cat population in 1974-1980.

SYNCHRONY OF OESTRUS PERIODS

Oestrus periods were more aggregated when measured within female groups, than between groups (Tab. 1). Only the first oestrus period of the year was tested for aggregation, since the timing of the second oestrus was dependent on the first one, and also on whether the female lost her kittens, or went through a full lactation (Christiansen 1978). Also, one-year-old females were excluded from this test, since their oestrus occurred significantly later than the older ones.

TABLE 1

Analysis of synchrony of oestrus in female cats. The breeding season was broken up in 6-days periods. Only the season for the first breeding of the year was considered (Jan 28th - March 31st), which gave 12 such periods. The occurrence of each female in oestrus was tested for co-occurrence with other females, in the same period. Consideration was taken whether the pair belonged to the same household group or not.

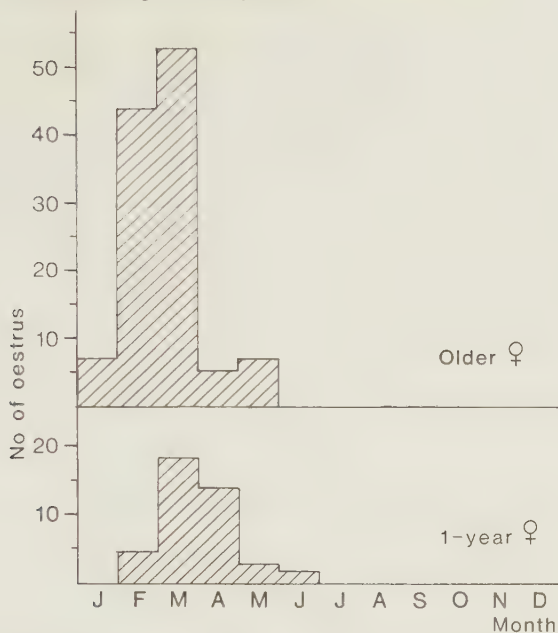
	Within the same group	Between groups
Maximum number of possible cases where two females could be in oestrus in the same 6-day period	75	301
Observed number of cases where two females were in oestrus in the same 6-day period (O)	15	28
Expected number of cases where two females were in oestrus in the same 6-day period, if oestrus occurred randomly $(75(\frac{1}{12})) * (E)$	6	25
Probability that O does not differ from E (χ^2 -test)	$p < 0.001$	N.S.

*and $(301(\frac{1}{12}))$ resp.

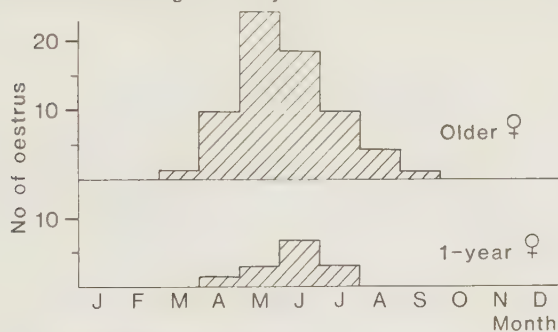
LOCATIONS OF COURTSHIP ACTIVITIES

Some females stayed around their home household, while others went off and stayed away, during their oestrus. There was a tendency, although not significant, that females living in groups that also contained males (usually related to the females) (Liberg 1980, Panaman 1981), more often went off from their home household during oestrus, than did females that had no males in their groups (Tab. 2).

First breeding of the year



Second breeding of the year



Third breeding of the year

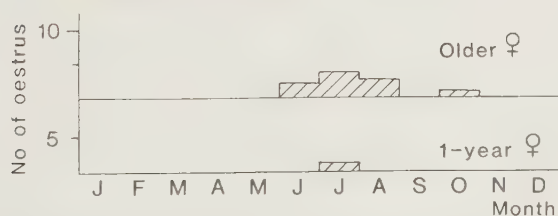


Fig. 2. Annual distribution of oestrus periods, divided up on first, second and third breeding of the year, and on two age-classes. Mean dates for onset of first oestrus of the year of older females, 1st of March, and of one-year-old females, 22nd of March, differ significantly (t-test, $p < 0.001$).

TABLE 2

Location of females during oestrus in relation to whether the female belonged to a group that also contained male cats.

	Females staying "at home" during oestrus	Females staying away from "home" during oestrus
Females having males in their group	6	9
Females not having males in their group	6	1

The distributions do not differ significantly (Fisher's exact probability test)

NUMBER OF COURTING MALES

Number of males observed to show interest for a certain female during a single oestrus period, ranged from one to five ($\bar{x}$ 2.3, median value 3) (Fig. 3). Number of males courting a female at any given moment was less, as males arrived to and left the courtship area irregularly all through the oestrus.

TYPES OF COURTING MALES

During the courtship, the female often sat or, more commonly, laid on her belly, surrounded by a number of male cats. However, there was always one male staying clearly much closer to the female, than any of the others, usually within one meter from her. This male I termed "the central male" (CM). If there were other males present, they maintained more peripheral positions. They were called "peripheral males" (PMs). As long as the female did not move, the CM did not either, while the PMs were more mobile. Besides lying still, which they also might do for long periods, they walked around, seemingly investigating the near surroundings, sniffing signposts and urine-marking, and sometimes closing up to the central pair, and then going off again. PMs now and then also left the courtship area, sometimes for only a few minutes, sometimes for longer periods, or even for the rest of that oestrus.

Often the female changed position, travelling short distances, making circuits and coming back to the same place, or in some cases making long excursions of up to several hundred meters

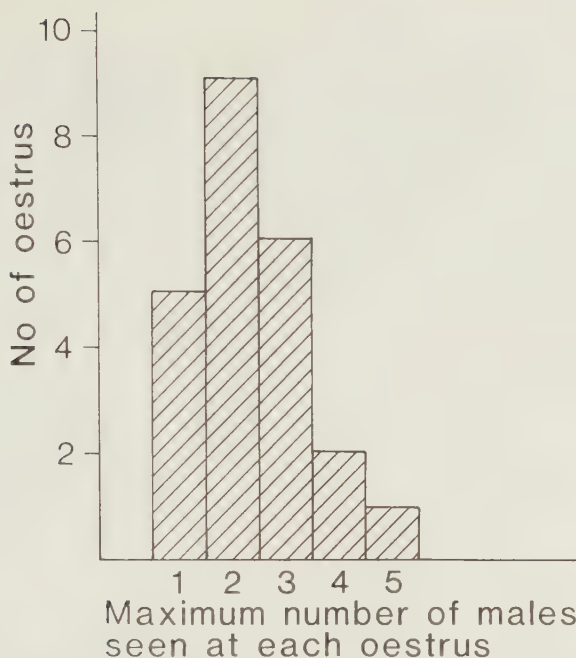


Fig. 3. Frequencies of number of male cats observed courting a particular female during the same oestrus.

("flirt walks", Leyhausen 1979). On these occasions the CM walked close behind her, often with his nose just a few centimeters from her rump. The PMs sometimes, but not always, participated in these walks. Sometimes the female made sudden and quick rushes, during which the CM occasionally lost contact with her, at least temporarily.

TABLE 3

Types of aggressive behaviour displayed between different males during courtship.

Status of males involved	Types of aggression					Σ
	Fights	Chases	Vocal duels	Threats, no or slight vocalization	PM repelled, no open aggression	
CM - PM	2	3	6	7	6	24
PM - PM	0	1	1	3	0	5
Σ	2	4	7	10	6	29

MALE AGGRESSIONS DURING COURTSHIP

Twenty-nine aggressive acts were recorded, 24 of these were between the CM and a PM (Tab. 3). Most aggressions occurred when a PM came too close to the CM or the female. Usually then, a threat from the CM was enough to deter the approaching PM. Sometimes the conflict escalated to a vocal duel. In only two cases was a full scale fight observed during courtship. In one case it happened when a former CM had lost his position, and took it back from another relatively strong male. The other occurred when a male, that usually held a CM position in several households in his central home range, challenged a CM in a peripheral household. Another three fights, that occurred during the courtships under observation, but when the observer was absent briefly, were reported by the cat-owners. All three were between males, that held CM positions in different female groups.

REPLACEMENT OF CENTRAL MALES

In 17 cases, a replacement of the CM was observed. They took place in nine different oestrus periods. These exchanges were roughly of three different types (Tab. 4). The first was when a former CM took back his central position, after he had been off from the courtship area for some time, or after he had lost the female during a quick rush of the latter. Most of these take over were clearly aggressive, although they did not usually escalate beyond a threat display.

The second type was when a PM took over temporarily in the confusion that followed after the female had made a rush, and the former CM had lost his contact with her. This type was only observed twice. The third type occurred when a CM, that had held his position for some time, left the courtship area. Most of these occasions were not seen, but recorded afterwards, when they already had taken place. In the two cases, when the observer was present, it seemed as if the CM left out of his own will, and no aggression was observed.

COPULATIONS

Copulations were performed by the CMs only. Several matings were performed by very young males, that held their positions possibly only because there were no other males present. A total of 19 completed copulations were recorded in the total of 1855 minutes,

TABLE 4

Conditions under which males assume the position of CM during courtship. Males that held CM positions several times and held the CM position for long periods when in competition with other males in the same season were classified as dominant animals.

		Aggression seen during exchange of CM	Aggression not seen during exchange of CM	Observer not present during exchange
Dominant male assumes CM position		5	2	1
Subordinate male assumes CM position	during or after quick rush of female	1	1	-
Subordinate male assumes CM position	after former CM has left courtship area	0	2	5

during which females were under direct observation, that is one copulation per 98 minutes, or 15 per 24 hours.

Different reactions of the PMs during copulations, were recorded. Often PMs looked away, or even walked off when the CM copulated. In other cases they seemed completely indifferent to what happened. In one case, however, a PM rose and walked up to the mating couple. It is not known whether he intended to interfere, because just when he came up to the female, she terminated the copulation in the usual way, by wheeling round with a scream, and hitting out at the CM, whereby also the approaching PM jumped back.

Distribution of sexual status in the male cat population

In 1979, there were three males in the study area, that were recorded to have maintained a CM position in competition with other males at least once, (Tab. 5). One of these males died in August 1979, and in 1980 a new male had been recruited into the class of regular CMs. In that year another regular CM disappeared, but was not replaced by any new one before June 1981, when the study was terminated. Most of the PMs were actually cats that appeared as CM at other occasions or places that same season. There was a tendency, that a male that once had acquired a CM position at a cer-

TABLE 5

Sexual performance and conflict scores of all male cats, one year old or older, in the intensive study area. A male was given a CM score, only if he had held that position during more than half the time the courtship activities had been under observation. CM position held in the absence of other males are indicated by (h). Usually that type of courtship occurred in the male's own home household. A male got PM score if that had been his main status during a courtship.

N = number of oestrus periods studied.

Identity of male cat	Sexual performance			Conflict scores	
	CM position	PM position	Number of copulation	Victories	Losses
<u>1979 (N=6)</u>					
846	3	0	1	5	0
303	2	3	2	3	4
229	1	2	0	2	3
350 ¹	1	0	2	2	0
406	0	2	0	0	2
455 ¹	0	1	0	0	1
456 ¹	0	1	0	0	0
515	0	0	0	0	0
524	0	0	0	0	0
849	0	1	0	0	1
<u>1980 (N=8)</u>					
229	1	0	2	2	0
406	2	1	3	4	2
303	4	3	2	4	4
849	0	4	0	0	4
515	0	0	0	0	0
604	1 (h)	0	1	0	0
605	0	0	0	0	0
617	1 (h)	0	1	0	0
613	0	0	0	0	0
618	0	0	0	0	0
609	0	0	0	0	0
<u>1981 (N=5)</u>					
406	2		0	2	0
303	2	1	1	0	2
606			1	0	0
849	0	1	0	0	0
609	1 (h)	0	2	0	0
515	0	1	0	0	0
604	0	0	0	0	0
618	0	1	0	1	0
617	0	1	0	0	0
703	0	0	0	0	0
719	0	0	0	0	0

¹These males belonged to a peripheral household that was not considered in 1980 and 1981.

tain female cat household, maintained this position there for at least the rest of that season.

A few males were recorded to occupy only PM positions. There was also a large number of males, that were never seen to participate in courting activities together with other males. Such males are called "non-participants (NPs). Sometimes such males were seen to court, and even copulate with, females in their own household groups, but this always happened in the absence of other males.

Age and bodyweight in relation to sexual status of male cats
To analyse the importance of age and bodyweight on a male cat's sexual status, all males were classified as typical CMs, PMs or NPs for each season, depending on which had been their main position that season. A new classification was made for each season, which means that the same individual might appear in one class in one year and in another the next year, or might reappear in the same class in consequent years (Tab. 6).

TABLE 6

Age and bodyweight of male cats of different sexual status. Sample size in parentheses. p-values for no difference between means of bodyweight are indicated (Mann-Whitney U-test).

	Typical CMs	Typical PMs	Typical NPs
Mean age (yrs)	4,2 (n=6)	2,7 (n=10)	1,1 (n=9)
Age range	3 - 5	2 - 4	1 - 2
Mean body weight (kg)	5,4 (n=8)	4,1 (n=6)	4,0 (n=10)
Weight range	4,9-6,0	3,6-5,1	3,4-4,7

Most NPs with known age were one year old; only one was two years old. A small number of NPs were feral cats that had immigrated into the area, and whose age was unknown. One of them must have been at least two years old in 1979, when he was still an NP. The average bodyweight of NPs was the same as that of PMs, but the latter were generally older, between two and four years. The CMs were the oldest males, three to five years old, and they were also the heaviest ones, weighing on average 35 % more than

the other categories.

DISCUSSION

PREDICTIONS FROM SEXUAL SELECTION THEORY

In developing his Sexual Selection theory, Darwin (1871) noted that commonly in nature, male animals compete strongly for mates, while females are more choosy in selecting their partners. This observation does not apply to all animal species, however. Recent theory is more exact, and predicts intensive competition between members of one sex, when most of the parental investment in the offspring is performed by the other sex (Trivers 1972, Emlen & Oring 1977). In mammals the large investors are usually females, and the competitors are males (Clutton-Brock and Harvey 1978). In species like the domestic cat, where the male's only investment in the offspring is the genes, that he conveys with his sperms, female choice should be based on an assessment of the quality of these genes in contributing to a viable and sexually successful offspring. In the male on the other hand, one should not expect a strong discrimination about whom to mate with, but an intensive competition for mating opportunities. The very competitive ability of the male would be one of the few cues about the male quality, that would be available for the female. One would therefore expect to find female behaviour patterns that increased the competition of the males (Halliday 1978).

TIMING OF OESTRUS

Timing of oestrus, especially in relation to other females, is a trait that both sexual and natural selection might act on. Synchrony of oestrus in females might lower the competition between males, by increasing the "Operational Sex Ratio" (OSR = average ratio of fertilizable females to sexually active males, Emlen and Oring 1977), while spacing out of oestrus between females would have the opposite effect, namely increasing male competition. Felids are able to time their oestrus in response to social factors, as was shown by Bertram (1975) in pride-living lions, where there was an oestrus synchrony between females of the same pride. In that case it was in the interest of the females to reduce competition between pride males, as fighting among them might be dangerous or fatal, and thereby lower their ability to

prevent outsiders to take over the pride. Such a take-over always reduced the fitness of the females through infanticide, stress-induced abortions etc.

Spacing out of oestrus periods did not occur in female cats living in the same group, where one would expect the strongest social influences on the timing of oestrus. On the contrary, there was a significant aggregation of oestrus periods within the groups, that did not occur between groups, and therefore is not likely to have been environmentally induced. If there at all has been any sexual selection for spacing out of oestrus periods, other selective forces, favouring the opposite tendency, might have been stronger e.g. advantages of communal care of, or communal defence of small kittens (see discussion on infanticide in next section). Macdonald and Apps (1979) found indications that kitten survival increases, if there are more than one lactating and caretaking female in the group, when kittens are small. Bertram (1975) claimed that food competition from older cubs, also might have been an important selection pressure for synchronized births. Such a selection might also be operating in cats, where there, at least in large groups, is an intense competition for food.

FEMALE BEHAVIOUR

Leyhausen (1979) claims that female cats in oestrus do not always prefer the most dominant male in a courting company, but might pick a subordinate male to mate with. In my study nothing indicates that a female would refuse to mate with whatever male happens to be the most competitive of those who court her. It is also hard to understand how such a behaviour would have evolved. However, the observed habit of the courted female to move around frequently, and sometimes making sudden rushes, certainly caused a lot of confusion and reshuffling among the courting males, and occasionally also gave a lower ranked male opportunity to mate. Still I would interpret this behaviour as primarily a means for the female to increase competition among males, as it might break a dead-lock, and force the CM to defend his status on a more equal basis, than when he is holding his position during an established situation. It is possible that this causes an asymmetry of power and advantage to the CM (Maynard-Smith and Parker 1976). But there is of course also the possibility, that the female with her rushes really wants to shake off a not-wanted CM, at least

temporarily, and be able to mate with some other male. This might actually be another part of a female's strategy, a strategy to decrease the risk for infanticide by males (Eaton 1978). The more uncertainty a female creates about who is the father of her litter, the fewer males would there be, that would be inclined to kill her kittens. Occurrence of infanticide has not been confirmed during seven years of intensive study of the actual cat population, but several instances have been recorded where females, alone or two together, have driven off both foreign males, and males of their own group, while the females had young kittens. This might be an indirect evidence for male infanticide.

Another motive for a female to get rid of a certain male, and prefer another, even if he has lower social status, would be if the dominant male was a close relative to the female. Very little is known about inbreeding depression in domestic cats, and, therefore, it is hard to judge how strong a selection force against inbreeding would be. Females in households where males also live (usually closely related to the females, brothers, sons etc. (Liberg 1980, Panaman 1981), had a stronger tendency to leave their home during oestrus than did females with no males in their home household (Tab. 2). This difference was not statistically significant, however. Such a behaviour might be an incest avoidance device.

Eaton (1978) hypothesized that the high copulatory frequency in many felids is a way for the female to assess male vigour or to lower the chance for competing females to mate with the same male, by exhausting him sexually. He had poor data on the copulation rate for housecats, but indicated that it would be somewhere in the range of 10 - 20 per day on based observations of his own cats. This corresponds well with the observed frequency of 15 per day in my study. Certainly this could be a way to test the vigour of the male, in addition to direct competition with other males she already has forced upon him. Whether such a copulation frequency also is enough to exhaust a healthy male is difficult to determine. ACM that had held his position for a while had a tendency to lose interest in the female and leave her, but this could be a strategy of a dominant male to maximise the number of females to be fertilized by him. This will be discussed below.

MALE AGGRESSIONS

Male cats determined their social status through aggression, sometimes escalated to full fights. Most aggressive encounters observed in my study were between individuals that had previous experience of each other. It is quite likely, that fights are more frequent among males making their first assessment of each other (Leyhausen, 1965).

Data of the present study do not permit a complete analysis of aggressions in relation to conflict theory (Maynard-Smith 1974, Parker 1974, Maynard-Smith and Parker 1976). As would be predicted, however, it seems as if conflicts are more often escalated when the opponents are of more equal strength, than in strongly asymmetrical situations. Also, conflicts were more frequent, and escalations more common, when higher gains and losses were at stake (a PM challenging a CM for his possession of the female), than when matters of less importance were settled (status between PMs).

A DOMINANT MALE STRATEGY

Female domestic cats are attractive to males for 6 - 8 days during an oestrus cycle. They allow copulation during the last 4 - 6 days. They are induced ovulators, with ovulations occurring 24-50 hours after copulation. More than one copulation are necessary to induce ovulation (Paape et al. 1975, Scott 1970, Burke 1975). It is likely that the chance of fertilization increases sharply during the first few hours after the first copulation, stays high during the period up to the ovulation, and then falls off slowly. The problem facing a strong male that maintains dominance in several female groups is that several oestrus periods are likely to overlap in time due to chance, in spite of the lack of synchrony between different female groups, especially if there are many females in his domain. A dominant male therefore runs the risk that subordinate males might fertilize females while he is busy somewhere else. One way to minimize this risk is to stay with a female in oestrus only during the most optimal time for fertilization and then move off to other female groups to check the situation there. If the dominant male does not find other females on heat, the best thing is to return to the first female, and resume the CM position there. Such a strategy could account for the unprovoked withdrawals of CMs observed during this study, and maybe

also for the relatively frequent copulations of subordinate males. A similar system has been observed in the bankvole (*Clethrionomys glareolus*) (Hoffmeyer, pers. comm.) and in the anubis baboon (de Voore 1971).

RANKING OF MALES

Age and size are important factors in determining social status among individual animals (Trivers 1972, Halliday 1978, Brenner et al. 1978). Among male cats, age seems to be the most important factor because no individual managed to attain a stable CM status before the age of three years, few before the age of four. Male cats did not automatically achieve high status, when growing old, though. Also bodyweight might be important. Feral male 849 was at least 4 years old in spring 1981, but still had not managed to hold a CM position. His bodyweight by then was 1 kg lower than the average weight of the typical CMs. Even other factors might be of importance. Male 515 was three years old in 1981, and also a large cat, weighing more than the average of typical CMs. Still he had not been seen to participate in more than one courtship, and that was in his own home household, where he behaved like a very "timid" PM. He disappeared from his home in late spring 1981, and it is believed that he had dispersed. This cat was much intimidated by his one year older household mate, male 406, with whom he also was related. The reason for the failure of male 515, might simply have been, that he grew up in one, for him, unfavourable situation when the dominant position was already occupied by a cat that he could not defeat. His best alternative might then have been to emigrate.

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REPRODUCTIVE SUCCESS IN MALE CATS IN RELATION
TO SOCIAL STATUS

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ABSTRACT

In a rural domestic cat population in Southern Sweden, female cats lived in stable groups, each group attached to a certain human household. Males compelled for mating opportunities. A small number of males, called Breeders, maintained mating priorities in exclusive female groups. Older males acted antagonistically towards younger males, when the latter reached the age of 10-14 months. These young males were thereafter called Novices. Novices avoided confrontation with dominant males. Some of them emigrated as a result of agonistic behaviour. Dispersers assumed a feral mode of life, often away from female groups, thereby minimizing contact with dominant males. These emigrants were called Outcasts. At the age of two or three years Novices and Outcasts, started visiting female cat households more frequently, and participated in courtship of females, and although still usually beaten by Breeders, did not always try to avoid them, but confronted them in open contests. Such males were called Challengers. For each male in each season, reproductive success was measured in the form of a paternity index, based on behaviour and kitten inheritance of coat colours. There was a close positive correlation between dominance and paternity index. Breeders had the highest indices about double that of Challengers, and four times higher than Novices and Outcasts. Breeders were partially territorial, defending their ranges probably to the most economical level. Female groups over which a male held Breeder status, were called his dominion. Breeders also visited female groups included in other Breeders' dominions. Possibly they thereby increased number of matings, but it was argued that they in this way prepared for later take over of these peripheral groups.

INTRODUCTION

The mating system of an animal population is ultimately determined by ecological factors like quality, distribution and abundance of food (Emlen & Oring 1977). In most carnivores, individuals are widely dispersed, as a response to a scarce, unpredictable and well dispersed food resource. This reduces the possibility for one individual to monopolize many mates. The system would tend towards monogamy, if food resource was the only important selective pressure. But at the same time, like in many other mammals, the female carnivore often is capable of rearing her offspring without the aid of the male. This allows the male to spend more of his time in acquiring new mates, i.e. a trend toward polygyny (Trivers 1972, Clutton-Brock & Harvey 1978). In most felids, polygyny occurs, but in a mild form, i.e. one male does not monopolize a large number of females. Probably, the most intense intrasexual selection for mate acquiring ability in felids occurs in the lion, Panthera leo, where the clumping of females in prides intensifies competition between males (Schaller 1972, Bertram 1975, Bygott et al. 1979). The other extreme might be found in solitary, low density felids like the mountain lion, Felis concolor (Seidensticker et al. 1973). The domestic cat

probably is somewhere between these extremes. It originates from a solitary, well dispersed ancestor, but is now often living in high densities, and with females occurring in groups (Liberg 1980, Panaman 1981).

In another paper I have shown that a rural cat population in southern Sweden indeed was polygynous, and that there were large variations between males in mating frequency (Liberg 1981c). Success in acquiring mating opportunities was positively correlated with age and bodyweight. The present paper examines reproductive success of male domestic cats in relation to social status, estimates determiners of social status, and describes mechanisms through which male cats maximized their reproductive output. Dispersal was common in young adult male cats (Liberg 1980). Because it seemed to have an intimate connection with male competition for mates, I have investigated why young tomcats leave the protection, and sometimes the affectionate love, of their owners.

The study was started in 1973, but most of the behaviour data are from the period August 1977 - August 1981.

STUDY AREA

The study was performed in the Revinge area in Southern Sweden. The area and its cat population has been described in detail in Liberg (1980, and 1981b). The area (4500 ha) was previously used for agriculture, but since the middle of the 60's it is used for military training and cattle grazing. It will be referred to as "The Revinge area". The population study of cats has been conducted in the southern half of the area (2000 ha), and will be referred to as the "Population Study Area". Finally, most of the behavioural data pertain to a small (500 ha) area in the western part of the "Population Study Area". This area is called "The Core" (Fig. 1).

THE CAT POPULATION

Some characteristics of the cats in the "Population Study Area" will be given as a background.

- 1) The density of cats has been fairly stable in 1973-1981, with approximately 3 cats per km².
- 2) The basic social unit was the female group, always attached to



Fig. 1. Revinge area, and the sub-areas; "the Population Study Area" (dashed outline) and "the Core" (dotted outline). Solid squares are households to which female cats were attached at least some time between 1978 and 1981. In "The Core" names of households are given. The Center household moved from I to II in 1979. The villages of Revinge (in north) and Hällestad also are denoted.

a human household. It ranged in size from one to seven closely related females. It sometimes contained a variable number of adult males, also related to the females and to each other, and finally there might occur kittens.

3) Almost all females stayed in their maternal group until they died. Only a small fraction of females emigrated, and then they usually started a new female group at a vacant household.

4) Most males dispersed before the age of three. Many of them established themselves as self subsistence feral cats, not attached to any one human household. This tendency decreased after 1977, when the wild rabbit population crashed. Rabbits were an important food resource for feral cats (Liberg 1981a,b).

5) Females shared small communal home-ranges, rarely exceeding 50 ha. Adult males had much larger ranges, especially feral cats.

6) When a female was in heat, she was usually courted by several males. There was always one male that stayed closer to the female than the other attendants, and who performed all copulations. This was called a Central Male Position (CM). The positions of other courting males were termed Peripheral Male positions (PMs). These terms were, and will be, referred to, only as positions during a certain courtship, and not as permanent status attributes of any certain male cat. Sometimes a new male assumed the CM position either by defeating the former CM or after an unprovoked retreat of the former CM.

METHODS

Numbers, population composition and turnover, mortality, natality, weights, and growth, as well as coat colours and other specific data on individual cats, were obtained 1) through frequent and repeated visits in cat-owning households, 2) by trapping and marking, 3) by searching for and inspection of litters, 4) by night-counts with spotlight and 5) by field observations of cat behaviour, with and without the aid of telemetry. These methods are described in Liberg (1980), von Schantz & Liberg (in press) and Liberg (1981b,c).

RADIO TRACKING

Collared transmitters were used having a construction as described by Terter et al. (1964). Frequency was 27 MHz. The receiver with a loop antenna could be carried and handled by hand. Equipment was delivered by Televilt, Stockholm. Recorded data were: Individual cat number, date, time, location, habitat, two different sets of activity code, number of minutes observed, scent marking, social and hunting behaviour. In some cases single locations were obtained, at other times the same cat was followed for several hours or even days. When several cats were fitted with transmitters in the same area, a modified focal animal sampling was used (Altmann 1974). We tracked the focal animal, for a period of twelve or twenty-four hours. It was followed continuously as long as it was active. If it was resting for a period more than half an hour, we turned to "the next animal on the list" and tracked that individual if it was active and so on. A point check of all cats fitted with transmitters was performed at least once every hour.

ANALYSIS OF RADIO DATA

All data were punched on data cards, and treated in a Univac computer. Testing for activity types was made on a sample of radio data, where there was a minimum of 30 minutes between consecutive recording. Location points were plotted by a GD3 programme. Consecutive points on the same location were treated as one point. Ranges were drawn by the convex polygone principle (Mohr & Stumpff 1966). Range size was computed by the formula suggested by Jennrich and Turner (1969).

RECORDING DOMINANT-SUBORDINATE RELATIONSHIPS

Dominance-subordination was determined in two main types of encounters between male cats:

- 1) Open aggression. This included fights, threats, vocal duels and chases (Leyhausen 1979, de Boer 1977, Beadle 1977). Sometimes several of these behaviours followed each other in succession, e.g. vocal duel-fight-chase, but they were still recorded as one encounter.

2) Avoidance. These were encounters, where only one of the antagonists, i.e. the subordinate, revealed the dominance relationship. They included unilateral defensive behaviour, such as crouching when a dominant approached or passed closely, and they also included hiding and sneaking away or even flight from an antagonist, without any preceding open aggression from the latter.

BREEDER STATUS

A male cat that upheld mating priority in a certain female group for more than just during one oestrus of one female, was called a Breeder of that group. As not all oestrus periods in all groups were kept under observation an indirect method for determining Breeder status was used. Three conditions should all be satisfied for a male to be classified as a Breeder:

1) The male should visit the household of the actual female group regularly. For males living in the group, this criteria was met automatically. For foreign males this was checked by telemetry, and for non-radioed males by reports of the people in the household. The latter method was only used when the identity of the male was wellknown by the resident people. (Through my frequent visits with detailed questions about both their own and foreign cats, most of the catowners became increasingly interested in cat behaviour, and greatly improved their observational ability.)

2) The male should at least once have been seen to hold a CM position in the female group in the season under consideration. Even here, cat owner reports could be used, but they should include an observation of copulation, to avoid misinterpretation of CM and PM positions.

3) The male should never have been seen to be dominated by another male in the group during the assumed Breeder's period of tenure, but he should at least once have been seen to dominate another male in that group. Again cat owner reports could be used, but only if they were detailed and could identify the cats involved. Further, in such contests only fights and chases were considered as evidence, because of the unambiguous nature of who was the winner.

I did not classify a male as a Breeder if all three criteria were based exclusively on cat owner reports. At least one of them should have been confirmed by me or my field assistants.

Determination of which male cat could have sired a certain litter, was based on a combination of genetic information i.e. inheritance of coat colours and behavioural data. Most colour variants are determined by gene actions from single loci (Robinson 1977). In the present study, phenotypes determined from six loci were used. Four of these have recessive mutant alleles, agouti - non agouti (A,a), mackerel tabby - blotched tabby (T,t^b), full colour - diluted colour (D,d) and short hair - long hair (L,l). One locus has a partially dominant mutant allele, piebald spotting (S,s) where S stands for the mutant. And finally I used the dominant sex linked allele for orange colour, O, situated on the x-chromosome, making male bearers (OY) and homozygous females (OO) all orange, while heterozygous females (XO) become tortoiseshell coloured (Robinson 1977).

There are at least two serious drawbacks with this method of determining kinship, compared with electrophoretic enzyme analysis (Ayala et al. 1980, McCracken et al. 1981); 1) It is rarely possible to determine whether a carrier of a dominant gene is homo- or heterozygous. 2) Genes on certain loci might mask the effects of genes from other loci through epistasis. It is for example impossible to see whether an orange cat is an agouti or a non agouti. Sometimes these problems were sorted out by knowledge of the mothers' phenotype. Also, in females, the phenotypes of their kittens might reveal recessive or masked alleles.

The paternity index for a male during each breeding season was the proportion of all litters born in "the Core", that could be identified as possible offspring after a three step procedure: 1) First, litters born by females living outside the range of the male were excluded. For males not radiotracked, information from catowners and also my own casual observations of cat movements in the area, were used.

2) Litters, where observation of courting males during the mothers' oestrus indicated that the questioned male could not be the father, were also excluded.

3) For litters that had not been excluded through the first two steps, a coat colour inheritance analysis was performed, and litters, with phenotypes that could have been inherited neither from the mother, nor from the questioned male, also were excluded.

The second step was only used in those cases where a large proportion of the courtship, during which the litter was sired,

had been observed. The paternity index indicates maximum number of litters that could have been sired by the male.

DEFINITIONS

All cats described in this study belong to the species Felis catus L. Different terms will be used to denote different categories of cats:

Domestic cats (syn. housecats): Cats that are attached to a certain human household, where it is recognized by the people as their cat, and offered food regularly.

Feral cat: A cat without connection to a certain household, usually derives most of its food from its own hunting.

Home cat: A cat that belongs to the household or female group under consideration.

Novice, Outcast, Challenger, Breeder: Reproductive stages of male cat. Definitions are given in the first part of Results.

Central Male, Peripheral Male (CM, PM): Positions that a male cat can assume while courting a female. Defined earlier in the "Cat population" section.

Dominant, Subordinate: Relative terms, describing the social rank of a cat individual, or a category, in relation to another.

Foreign cat: A cat belonging to another household or female cat group than the one under consideration.

NUMBERS AND NAMES OF INDIVIDUAL CATS, AND OF HOUSEHOLDS

All cats were given an individual number, that also indicated the year of birth. Cats with number 1-99 were born before 1974, numbers 101-199 were given to cats born in 1974, 201-299 to cats born in 1975 and so on. Cats whose year of birth was unknown (usually immigrating feral cats) were given numbers 801-899. Some male cats in "the Core" were also given names. Here the first letter in the name indicated year of birth, C meant 1975, D 1976 and so on, while S designated an unknown year of birth.

The same name as was used for a household, was also used for the female cat group living there.

RESULTS

FEMALE GROUPS AND MALE CATS IN "THE CORE" 1978-81

The number of households with female cats increased from three to eight during 1978-81, and the number of adult female cats varied between 7 and 18 (Table 1, Fig. 1). This was an unusual variation, compared with the situation in the Population Study Area over the period 1974-81 (Liberg 1980 and unpubl.). No feral female cats were recorded in "The Core" in 1978-81.

TABLE 1

Female cat groups attached to households in "The Core" in 1978 - 1981.

Name of household	Number of adult females in each group by 1 April each year			
	1978	1979	1980	1981
Eastwood	0	2	2	1
Center	4	5	6	6
Offside	0	1	1	1
School	1	1	2	3
Westend*	-	2	-	-
Meadow	2	2	3	1
Water Mill	0	0	1	1
Marsh	0	0	1	1
Highway	0	2	2	2
Total number of females (excluding Westend)	7	13	18	16
Total number of groups (excluding Westend)	3	6	8	8

* Outside regular study area. Only considered in 1979 when one of the males from "The Core" visited this household and courted females there.

Also number of adult male cats increased in "The Core" during 1978-81. There were between five and nine male housecats and between one and three feral males in the area during this period (Fig. 2). Thirteen different males were radiotracked in one or several periods during 1977-1981 in "The Core". Beside these, data were also taken from another five males radiotracked in different parts of the Revinge area in 1975-1977 (Fig. 3).

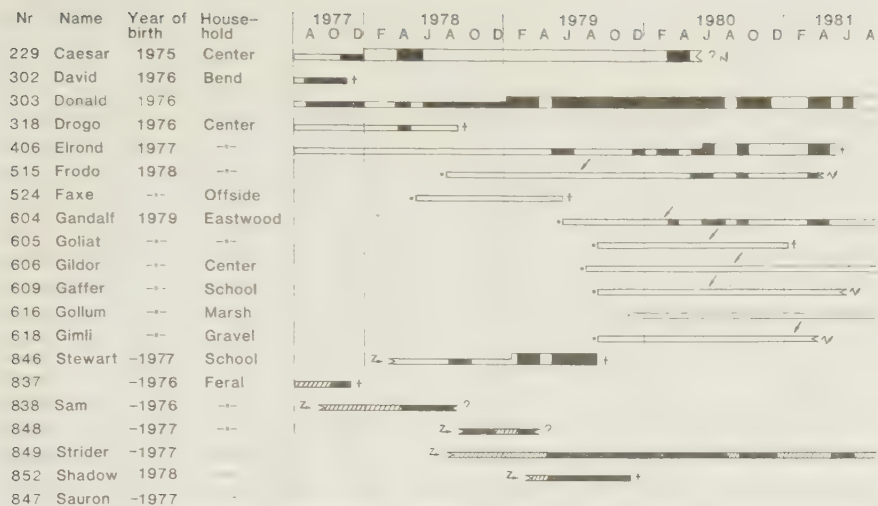


Fig. 2. Male cats occurring in "The Core" in 1977 to 1981. Males born in 1980 and 1981 are excluded. Thin bars indicate a subordinate status, thick bars indicate Breeder status, open bars indicate domestic cats, and hatched bars indicate feral cats. Solid sections of bars indicate periods of radiotracking.

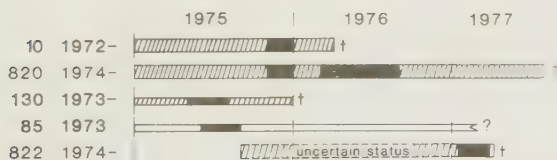


Fig. 3. Male cats radiotracked before August 1977, or outside "The Core", symbols as in Fig. 1.

Breeder

Criteria for classifying a cat as a Breeder are given in Methods. Basic data for the analysis are given in Appendix I. In any particular female group, there was only one Breeder at a time, except in the Center group in 1979, where two males, Caesar and Stewart, seemed to be of about equal strength, and both were qualified as Breeders in that group. Actually, coat colour inheritance data for one litter born in the Center group in 1979 indicated that most probably these two males shared paternity of that litter.

The "dominion" of a Breeder was defined as those female groups where he held his mating priority. In a geographical sense, the dominion meant the households where these females lived, and their near surroundings.

Most Breeders held their status in a female group for at least one whole reproductive season. The possible change of Breeder in a female group usually took place between breeding seasons. However, in two cases such take overs were observed during a breeding season. One case was when Elrond attained a Breeder position in his own group, the Center, and in Eastwood, after that the former Breeder, Caesar, left the area in 1980. The other case was when Stewart defeated Donald in the Meadow group in 1979. This take over was violent, including fights and other aggressive behaviour.

In "The Core" during 1978-81, there occurred 22 different adult male cats (Table 2). Only five of these attained Breeder status, and there were never more than three Breeders in the area simultaneously. No male attained Breeder status before the age of three years.

By August 1981, the tenures of three Breeders had been recorded. One of them lasted for one breeding season, the second for one and a half and the third for two and a half seasons. The former two were terminated by death of the Breeder. In the third case, there was some evidence that the male left the area because he was forced out. Of the two males that still in August 1981 were keeping their Breeder position, one (Donald) had held his for three seasons.

TABLE 2

Adult male cats occurring in "The Core" in 1978-81, with number of female cat households included in each male's range (first figure) and number of female groups where each male was holding Breeder status (second figure).

Male identity							
No.	Name	Year of birth	1978	1979	1980	1981	Length of tenure (years)
229	Caecar	1975	3/3	4/2	5/2	-	2.5
303	Donald	1976	3/0	7/1	8/4	9/5	> 3
318	David	"	1/0	-	-	-	-
846	Stewart	before -77	2/0	4/3	-	-	1
838	Sam	- " -	3/0	-	-	-	-
404	Elrond	1977	1/0	2/0	2/2	3/2	1.5
849	Strider	before -78	-	2/0	5/0	5/0	-
847	Sauron	- " -	-	-	1/1	2/2	> 2
515	Frodo	1978	-	1/0	2/0	3/0	-
524	Faxe	- " -	-	1/0	-	-	-
604	Gandalf	1979	-	-	1/0	4/0	-
605	Goliath	"	-	-	1/0	-	-
606	Gildor	"	-	-	1/0	1/0	-
609	Gaffer	"	-	-	1/0	2/0	-
613	Gloin	"	-	-	1/0	-	-
616	Gollum	"	-	-	1/0	1/0	-
618	Gimli	"	-	-	0/0	1/0	-
703		1980	-	-	-	1/0	-
710		"	-	-	-	1/0	-
716		"	-	-	-	1/0	-
717		"	-	-	-	1/0	-
719		"	-	-	-	1/0	-

Novices

Young males usually lived peacefully with other males, both foreign males and those belonging to the same maternal group, up to the age of 8-12 months. Then, often very dramatically, aggression started to play an important role in their lives. Most often it first appeared as attacks on the young male, by the resident Breeder. But sometimes the aggressive "debut" of the adolescent was in a contest with an age peer or an older group mate. There was a slight tendency, that the aggressive "debut" occurred later

TABLE 3

Age at which Novices were first attacked by dominant males, mostly the resident Breeder. There was no statistically significant difference between Novices living in households where the resident Breeder also was based, and Novices living in other households (t-test, two-tailed, $t = 1.4$, 17 d.f., $p > 0.05$).

Age (in months) at which Novices was first attacked by dominant males	Novices born in the resident Breeders' own home-group	Novices born in other female groups
8	0	1
9	0	1
10	0	5
11	2	1
12	1	2
13	2	0
14	1	3
$\bar{x}$	12.3	11.1
S.D.	1.2	2.0

in the life of young males belonging to the same group as the resident Breeder, as compared to adolescents in groups where the Breeder was a foreign male (Table 3).

The aggressive "debut" coincided with the age, at which male cats attain sexual maturity (Fox 1975). After the aggressive "debut" the young cat is classified as a Novice.

In the first period after the "debut" the Novices were frequently attacked by older males, and after a short time, they usually developed a strong fear for dominant males.

For example, in Eastwood the people immediately knew when the local Breeder, Elrond, came on a visit, because there was always a typical "bang" when their own Novice, Gandalf, invariably jumped down in his customary hiding place.

Sometimes Novice turned so nervous that they would flee from any strange cat directly on sight. When a Novice was in the vicinity of a Breeder, or a more dominant Novice, he kept "a low profile", to avoid the aggressor(s) as much as possible or to keep him under close watch. An example from the field notes:

"June 10th 1980. At 16⁵⁰ Frodo, a two year old Novice, comes upon the Breeder Elrond, who sleeps in the garden of their communal household. Frodo lies down

on his belly, and keeps Elrond under continuous watch. Elrond wakes up at 17⁰⁰, rises relaxed, looks around briefly without giving Frodo a glance and then starts grooming himself, while Frodo crouches. At 17⁰⁵ Elrond lays down sleeping again, Frodo is still crouching."

However, there were also situations recorded when two males, that had been fighting bitterly recently, lay sleeping close to each other. But this only occurred with males that were group mates.

Novice movements, and Outcasts

Novices were the most mobile class of male cats. Three types of movements of Novices were recorded. Return movements, that temporarily brought the cat out of his normal day to day range, were called "exploratory trips". These were of various lengths, up to five km. Such movements were recorded for five different Novices. There was a tendency of these trips to be directed away from, rather than in towards, the core area of the resident Breeder in the home area of the Novices (Fig. 4).

The duration of these trips also varied, from a few hours, to several weeks and even months. Exploratory trips of very long duration graded into the next type of movements recorded, temporary dispersals. These were defined as movements where the cat assumed residency in a new area for more than six months, and then returned to its original home, and resumed residency there again. Two cases of this movement type were recorded in the Revinge area. In one, the cat assumed a feral mode of life from June 1975 to May 1976, in an area two kilometers from home, and then returned home and stayed there at least one year (Liberg 1980). In the second, the cat moved to a new household only one km away from home in August 1980, where he stayed over winter, and returned home in March 1981. In the end of summer 1981, he was again away for long periods, but this time making short visits to his old home at irregular intervals.

The third type of movement exhibited by Novices was permanent dispersal. This kind of movement has been treated in an earlier report (Liberg 1980), and data accumulated since then, support the conclusions made at that time. A large proportion of young male cats in the Revinge area emigrated from their natal household. Forty-four disappearances of young male cats were classified as dispersals, although far from all of them were confirmed. Only four cases were recorded, where a cat attained a Breeder

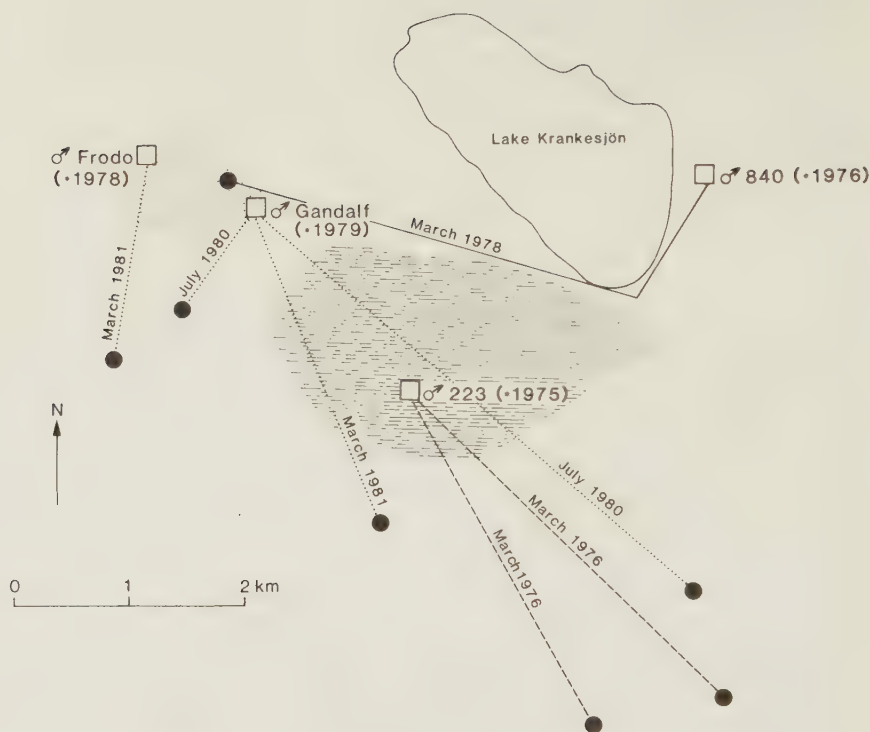


Fig. 4. Exploratory trips of Novices and the outlines of the resident Breeders' homeranges. For Novices 223 the resident Breeder's homerange is hatched, for Novices Gandalf and Frodo it is dotted. For male 840 neither exact status, nor outline of resident Breeder's home range were known.

status, while he was still living in his natal household. The dispersal was performed in the age of one to three years. Usually the dispersing male established himself as a feral cat.

Two tests were performed to find out whether dispersal was a response to dominant male aggression. In the first test dispersal tendency was compared between Novices living in households that offered good protection against the attacks of other male cats, i.e. household where the cats were allowed to enter the dwelling-house, and Novices not offered such protection. In the non-protective households all the young males, except one, emigrated in their second year. In the households providing the best protection only 20 % dispersed in the second year and 20 % of the males

even stayed long enough to attain Breeder status while still living in their natal group (Table 4).

TABLE 4

Age at which Novices emigrated from their home-household. The cats are arranged in three groups depending on the degree of protection offered by their natal household. Poor protection = households where cats were not permitted inside the dwelling-house. Intermediate protection = households where cats were permitted sometimes inside the dwelling-house. Good protection = households where cats always were permitted in the house. There was a significant effect on age of emigration dependent on the degree of protection offered by the households (Chi square summary within each cell outlined, $\chi^2 = 17.7$ d.f. = 1, $p < 0.001$).

Age at emigration (years)	Household's protection:		
	Poor	Intermediate	Good
1	20	4	3
2	1	3	6
3	0	1	3
Stayed to become a Breeder	0	1	3

In the second test, I investigated if dispersed subordinate males tried to avoid dominant males by staying away from places where they were likely to meet dominants. It was assumed that male cats occurring in the Revinge area, and not known to be resident domestic cats, were dispersers or post-dispersed cats. It was further assumed that bodyweight of these cats was correlated positively to social rank (see Liberg 1981c and next section in this paper). Finally it was assumed that the highest risk of encountering a dominant male would be near or at a household with female cats. The test consisted of plotting bodyweights of dispersed cats against distance from the place they were collected to nearest female cat household (Fig. 5). There was a significant negative correlation between these two parameters. This probably means that low ranked dispersers stayed away from the vicinity of dominant males.

It was this tendency of emigrants to settle at places away from the focal areas of social life that qualified them for the term "Outcasts". Outcasts' behaviour versus more dominant males,

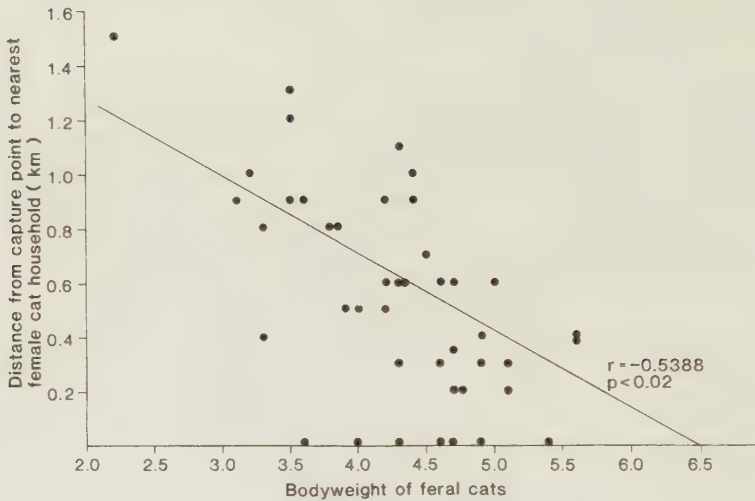


Fig. 5. Correlation between bodyweights of captured male feral cats, and distance from capture point to nearest female cat household.

especially Breeders, was similar to that of Novices.

Two cases have been recorded, where the disperser settled in another human household, instead of making it on their own as ferals. In both these cases females occurred in the households, but no adult males. However, in both groups the female cats were given contraceptive pills which keep them in constant anoestrus.

Challengers

When subordinate males, both Novices and Outcasts grew older, a gradual change in behaviour was observed. They did not always avoid or flee from Breeders, and they began to participate regularly in courtship, although mostly as Peripheral Males (PMs). These cats were called "Challengers". In an earlier paper, these cats were called "typical PMs", due to their frequent assuming of PM positions during courtship, but rarely a CM position (Liberg 1981c).

PROPERTIES OF DIFFERENT REPRODUCTIVE STAGES, AND
COMPARISONS BETWEEN THEM

Paternity index

A paternity index was determined for each male in "The Core" for the three breeding seasons of 1979-81. In 1981, indices were not determined for the one-year-old cohort, due to lack of data on their ranges.

Breeders had the highest average paternity index and Novices and Outcasts the lowest. Challengers had an intermediate index (Table 5).

No males had zero values. The reason might partly be that this index is a maximum value but this also indicated that Breeders did not completely exclude other males from breeding. On at least eight occasions a subordinate mated with a female, and many more matings were reported by owners, although not in such a detail that they could be regarded as unequivocal.

One of these cases of a young subordinate male mating is worthwhile reporting in some detail, because of the implications it might have for the possibility of kin selection, or degree of inbreeding avoidance or both in the male domestic cat. The Breeder male of the Centergroup in 1981 was a home male, Elrond. On the 5th of April a one year old female in the group, No. 701, was in heat. The litter she was born in was one of the few from the year before in which Elrond was the most likely father (the year before another male had been the Breeder in that group).

"When I arrived to the household at 12¹⁵, female 701 was courted by four males, Elrond, Donald (a foreign Breeder) and two younger home males, the three year old Frodo and two year old Gildor. Just when I arrived, there was a reshuffling of the situation, since all the cats were chased out of an outbuilding by the people of the household. During the confusion, Elrond was once seen to threaten the stranger Donald. Frodo left, and so did Donald and Elrond for a while. In the meantime, Gildor copulated once with the female while he was alone with her. Soon afterwards the female went into the outbuilding again, followed by Gildor. Shortly thereafter both Elrond and Donald appeared again. They approached the female, but Gildor maintained his Central Male position, lying just a few decimeters away from the female. Elrond and Donald lay a meter away. These positions were held for two hours, after which I had to leave. Gildor once mated with the female during this time, but probably the copulation was never fulfilled (no typical final reaction from the female). No tension was observed between the two older males. On the next day I observed the female for another three hours. At first Frodo lay close to her. Later Elrond appeared and assumed the CM position without any overt aggression. He followed the female for half an hour, after which he left her. She was soon again courted by Frodo, who was still with her when I left them. There was a great difference in the behaviour of Elrond and Frodo. Elrond had a relaxed and almost uninterested appearance when courting the female, while Frodo seemed watchful and nervous, looking around himself and especially backwards, all the time. Gildor and Donald did not show up this day."

TABLE 5

Paternity indices for males in "the Core" 1979-81. N = number of litters where coat colours of all kittens were determined. Caesar disappeared during the breeding season of 1980, so only litters sired, while he was still present, were considered for his paternity index.

Names and year of birth of male cats												
Breeding season	Stewart -1977	Caesar 1975	Donald 1976	Elrond 1977	Strider -1977	Frodo 1978	Faxe 1978	Gandalf 1979	Gildor 1979	Gaffer 1979	Gollum 1979	N
1979	0.60	0.45	0.25	0.15	0.15	0.10	0.05	0.10	-	-	-	20
1980	-	0.40	0.48	0.14	0.24	0.05	-	0.05	0.14	0-05	0.10	21
1981	-	-	0.36	0.36	0.21	0.14	-	0.14	0.14	0.14	0.07	14
Breeders $\bar{x}$ = 0.41 S.D. = 0.11												
Challen- gers $\bar{x}$ = 0.19 S.D. = 0.05												
Outcasts and Novices $\bar{x}$ = 0.10 S.D. = 0.04												

Visits to foreign female groups

Challengers visited foreign households with female cats more frequently than Novices did, but less frequently than Breeders (Fig. 6). Novices almost never visited such households, and Outcasts usually did so only when none of the resident females were in heat. Outcasts were the only class, that showed a higher frequency of resting than of activity while visiting female cat households. In contrast to Breeders and Challengers, Outcasts also visited female cat households as frequently in the non-breeding season, as they did during the breeding season. It seemed as if households with female cats were more significant to Outcasts as places where one finds mates.

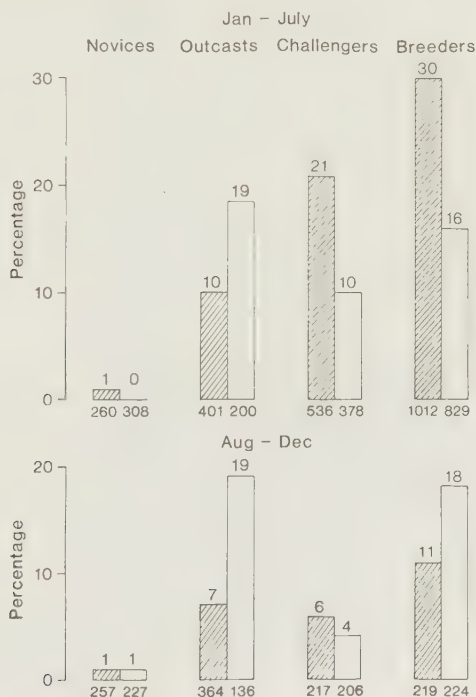


Fig. 6. Male cat visits to foreign female cat households. The four reproductive stages of male cats were considered. Average frequencies of time spent in female cat households are divided by "active" (hatched columns) and "passive" (open columns) time, on mating season (Jan-July) and non-mating season (Aug-Dec). Total number of location points of the different categories are given under each column. The columns show the percentage time spent in foreign female households, and percentages are given on top of columns.

Dominant-subordinate interactions

On many occasions when two male cats met or were together they behaved indifferently towards one another, or even amicable. In 64 encounters, however, a relationship of dominance could be determined. These behaviours ranged the whole scale from serious fights to nervousness or avoidance. 90 % of them occurred during the mating season, February to July (Fig. 7). Less than half of them (29) occurred during courtship. Most of them, however, occurred at or near households where female cats lived. A few occurred out in the field, probably as a result of two cats suddenly facing each other accidentally.

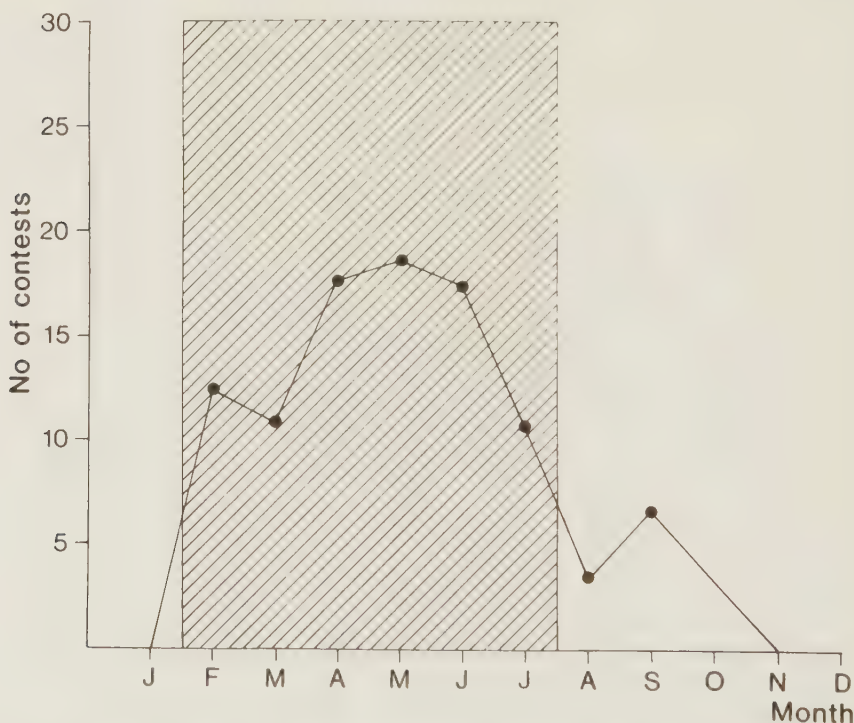


Fig. 7. Monthly totals of observed encounters between male cats, where dominant-subordinate relationships could be determined (see text for further explanation). Number of encounters are adjusted to total observation time per month. The shaded area shows the extent of the mating season.

Most of the contests involved Breeders, either contesting among themselves or dominating subordinate individuals. In three

cases, a Challenger dominated over a Breeder, but all three occurred in female groups where the Breeder was outside of his own dominion. Also a few cases were recorded when a Challenger dominated over a Novice (Table 6, Fig. 8).

TABLE 6

Dominant-subordinate encounters between male cats of different reproductive stages.

		Subordinates				Total encounters with dominance
		Breeders	Challengers	Outcasts	Novices	
Dominants	Breeders	17	17	13	10	57
	Challengers	3	0	0	4	7
	Outcasts	0	0	0	0	0
	Novices	0	0	0	0	0
Total encounters with subordination		20	17	13	14	64

Open aggressions were most common in Breeder-Breeder interactions and Breeder-Challenger encounters. Outcasts and Novices more often showed their subordinate status by avoiding direct confrontation with Breeders and Challengers (Table 7).

TABLE 7

Encounters between male cats where open aggression or avoidance behaviour were observed.

		Open aggression	Avoidance		
Breeder-Breeder	12	5	$\chi^2 = 0.50, p > 0.05$	$\chi^2 = 3.49$ $p = 0.06$	
Breeder-Challenger	9	8			
Breeder } - { Outcast Challenger } - { Novices	9	15	$\chi^2 = 0.44, p > 0.05$		

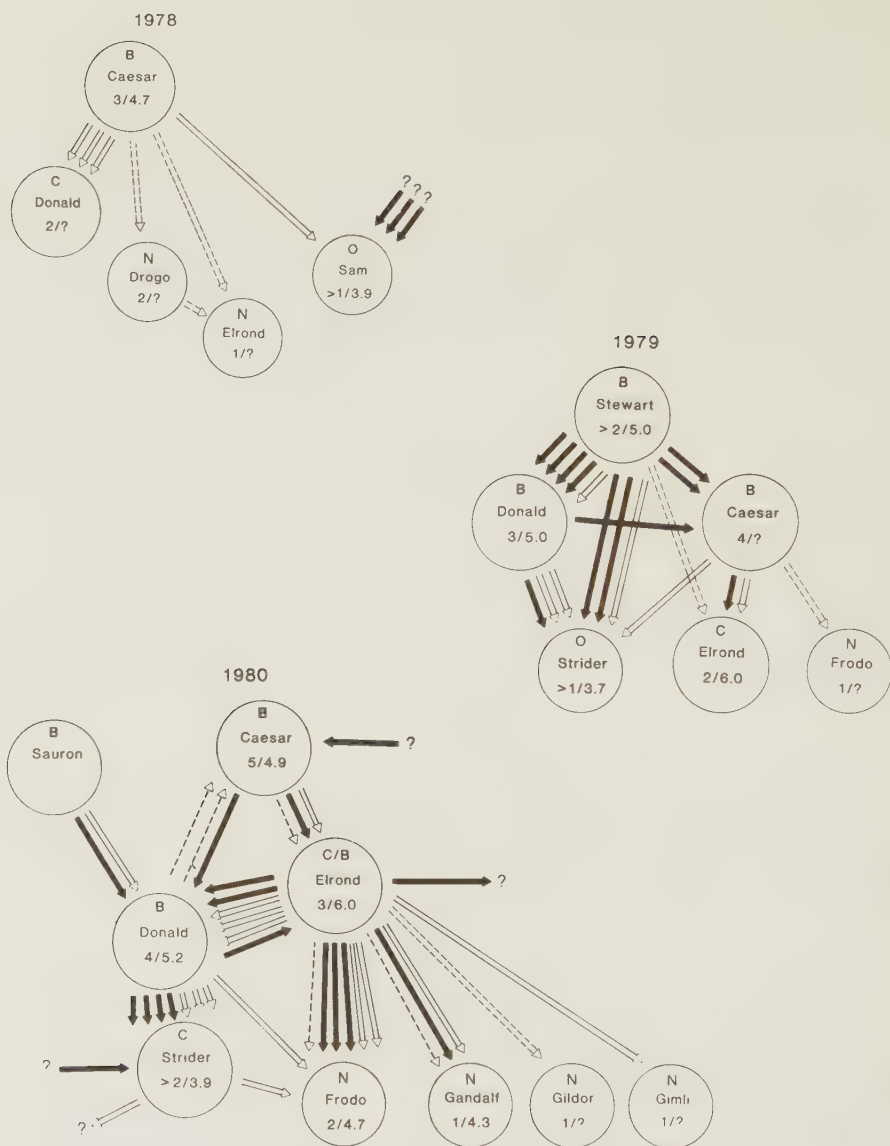


Fig. 8. Dominant-Subordinate encounters and relationships between individual male cats in "The Core" in 1978-80. Each circle represents one cat. Letter on top of name denotes status: B = Breeder, C = Challenger, O = Outcast and N = Novice. The figures below name give age/bodyweight (kg). Arrows point from dominants towards subordinates. Filled arrows denote open aggressions, open arrows denote avoidance behaviour by the subordinate. Simple dashed arrows denote aggressions reported by cat owners and believed to be reliable. Double dashed arrows denote permanent dominant-subordinate relations, based on many reports by cat owners of unidirectional dominance behaviour between cats.

The relative dominance of a male was site related. In 1979 and 1980 Donald was dominant over Caesar in the Meadow group, while the opposite was the case in the Center group (Fig. 8). This phenomenon could even affect the relationship between a Breeder and a subordinate male. In 1980, Strider, usually fled from Donald, or avoided him, when they met in the northern part of Strider's range. However, in an encounter in the southern part of Strider's range, Strider behaved in quite a different way, and stood his ground when Donald tried to force his way past Strider, who was lying at a door hole into a barn. Strider had used that area frequently for two years, while Donald recently had extended his range this far south. Also, in 1980 when females were in oestrus in Meadow in the northern part of Strider's range, he did not participate in courtship, but behaved like a Novice. But in the Highway group in the southern part of his home range, Strider behaved very challenging during courtship of females, although it was the same Breeder in both groups, i.e. Donald.

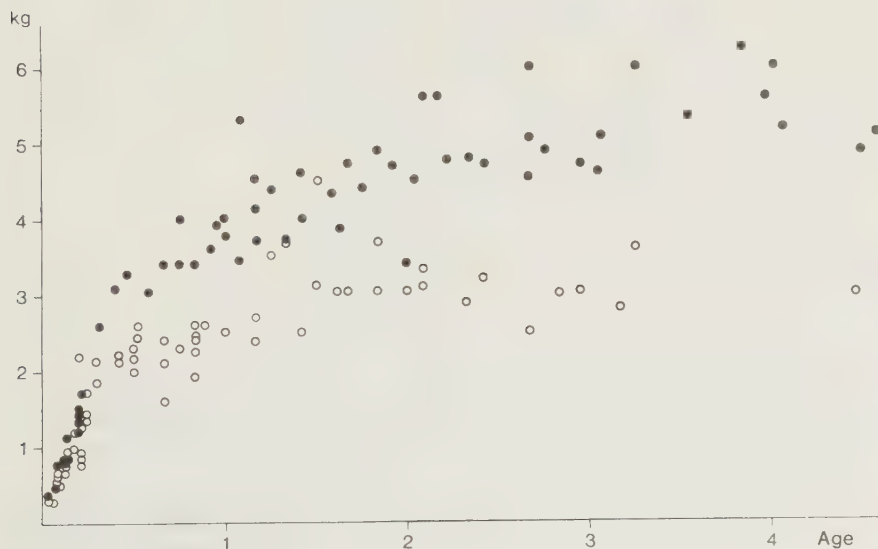


Fig. 9. Growth of bodyweights of cats in the Revinge area. Open circles = females, filled circles = males.

Male cats in the Revinge area did not attain full body weight, until they were at least three years old. This was in contrast to female cats, that increased little in weight after the age of two years (Fig. 9).

Age and bodyweight of male cats were both closely correlated to social dominance, measured as percentage "victories" of all contests recorded for each male. Age and bodyweight, respectively, were also significantly correlated to reproductive success (paternity index), but not as close as the correlation between social dominance and reproductive success (Table 8).

Home ranges

Annual home range size of male cats varied between 10 and 990 ha. Feral cats generally had larger home ranges than domestic cats. Novices had the smallest ranges and Outcasts had the largest. Number of females included in the home range was highest for Breeders, and lowest for Outcasts and Novices (Table 9).

Although Breeders had the highest variation in home range size, they had a relatively low variation in number of female cats included in their ranges, and even less variation of number of females in their dominions (Table 10). Outcasts had the least variable home range sizes, and Novices had the most variable number of females included in their home ranges.

There was no obvious sign of exclusiveness of the home ranges. All classes had overlapping ranges, both within the class, and between them (Fig. A, B, C). But within this general pattern of broad overlaps there were several indications of spatial avoidance. Novices tended to minimize home range overlap with those Breeders they had most contact with, clearly seen in Frodo's and Gandalf's ranges in 1980 (Fig. 10C). Similarly Outcasts responded towards aggressive encounters with other male cats by partially shifting their home ranges.

In 1978 Sam gradually shifted his home range eastward, possibly as response to clashes with other male cats in the western parts of his range.

In 1979, Strider occupied about the same home range as Sam the year before. In late May Strider also shifted his home range eastward, possibly in response to a couple of clashes he just previously had had with Donald and Caesar, two Breeders in that area.

TABLE 8

Paternity indices, frequency of "victories" (indicated the cat was dominant), age and bodyweight of individual male cats in "The Core" in 1979 and 1980.

r_s -values are Spearman rank correlation coefficients corrected for ties.

The males are ranked in order of paternity index.

Name	Year	Pat. index	% vic- tories	Age (years)	Body- weight (kg)
Stewart	-79	0.60	100	≥ 2	5.0
Donald	-80	0.48	47	4	5.2
Caesar	-79	0.45	50	4	4.8
"	-80	0.40	75	5	4.9
Donald	-79	0.25	44	3	5.1
Strider	-80	0.24	23	≥ 3	3.9
"	-79	0.15	0	≥ 2	3.7
Elrond	-79	0.15	0	2	?
"	-80	0.14	82	3	6.0
Gildor	-80	0.14	0	1	3.6
Gollum	-80	0.10	0	1	3.4
Frodo	-79	0.10	0	1	?
"	-80	0.05	0	2	4.7
Gaffer	-80	0.05	-	1	?

$r_s = 0.86$
 $p < 0.01$

$r_s = 0.82$
 $p < 0.01$

$r_s = 0.81$
 $p < 0.01$

$r_s = 0.87$
 $p < 0.01$

$r_s = 0.57$
 $p < 0.05$

By July, he was back in the western part of his range. He had two fights with another Breeder, Stewart, on the northern border of his home range, but this time no spatial response was observed. In August Stewart was shot by a hunter, and soon afterwards Strider extended his home range northward into a part of what had earlier been Stewart's range.

Breeders also shifted their ranges to some extent. Mostly this was noticed as differences in intensity of use or as extensions of their ranges as they incorporated new female groups under

TABLE 9

Home range sizes and number of female cats included in ranges for males of different reproductive stages.
The number of female cats included in dominions are given for domestic breeders.

Domestic cats					Feral cats				
Name	Year	Range size (km ²)	N locations	N females in range	Name or number	Year	Range size (km ²)	N locations	N females in range
Novices and Out-casts	Caesar	-78	22	1	837	-77	9.3	25	?
	"	-77	83	4	Sam	-78	7.9	251	2
	Donald	-77	96	2	848	-78	1.8	92	1
	Drogo	-78	26	4	Strider	-79	4.7	410	4
	Frodo	-80	105	9	Shadow	-79	7.7	38	3
	Gandalf	-80	89	2					
	$\bar{x}$	0.8		3.7		$\bar{x}$	6.3		2.5
	S.D.	0.6		2.9		S.D.	3.0		1.3
Challengers	85	-75	35	7	130	-75	3.1	62	?
	David	-77	58	4	Strider	-80	2.9	311	9
	Donald	-78	217	7					
	840	-78	28	?					
	Elrond	-79	156	7					
	$\bar{x}$	3.0		6.3		$\bar{x}$	3.0		-
	S.D.	2.1		1.5		S.D.	0.1		-
					N females incl. in dominion				
Breeders	Caesar	-78	88	7	10	-75	3.1	15	6
	"	-80	48	12	820	-75	3.3	25	7
	Stewart	-79	178	9	"	-76	9.9	118	9
	Donald	-79	218	14					
	"	-80	320	15					
	Elrond	-80	333	8					
	$\bar{x}$	3.8		10.8		$\bar{x}$	5.4		7.3
	S.D.	3.7		3.3		S.D.	3.9		1.5

TABLE 10

Coefficients of variation ($S.D./\bar{x} \cdot 100$) for home range sizes and number of female cats included in home range, in different stages of male cats.

	Coefficients of variation		
	Range size	Number of female cats in home range	Number of female cats in dominion
Domestic Breeder	97	31	22
Feral "	72	21	?
Domestic Challengers	70	24	-
Novices	75	79	-
Outcasts	48	52	-

their domain, but sometimes they also gave up part of their ranges.

Ceasar gave up the eastern part of his 1978-79 range in 1980, possibly due to his defeats there by Donald in 1979. Also, as was already mentioned, in the middle of 1980, Caesar left "The Core" altogether, and probably moved south.

Scent communication and travelling

All male cats urine sprayed frequently. Most spraying was observed during travelling. Breeders sprayed about twice as frequently per travelling time as the other classes. Often a cat sniffed the marking place before he sprayed, and sometimes sniffing was observed without marking. The ratio of sniffing per marking was higher in Novices than in Breeders. In the other classes, data were too few for comparisons (Table 11).

Cats mainly travelled along natural "lines" formed by hedges, tree lines, ditches, fences and small tracks connecting small woods, marshes, plantations and human dwellings (Fig. 11). Scent marking was frequent along these, while little marking was performed when cats cut across fields (Fig. 12). Spatial patterns of scent marking will be treated in detail elsewhere.

A: 1978

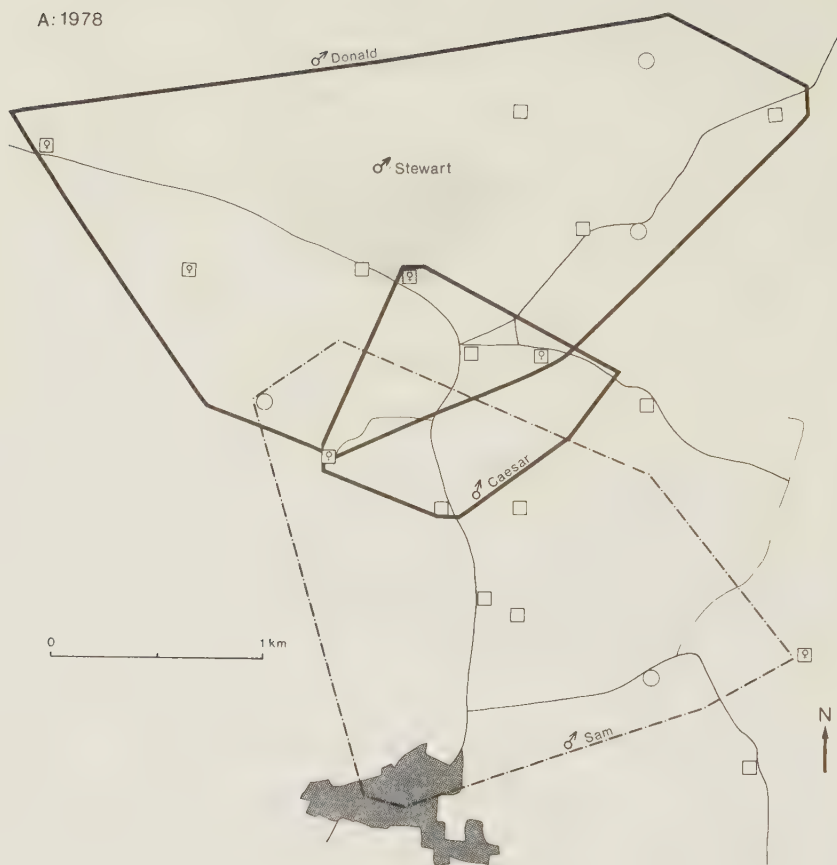


Fig. 10. Home ranges of male cats in "The Core". Thick lines indicate Breeder ranges, except for Donald in 1978, who was by then a Challenger. Dashed lines denote ranges of Outcasts, and hatched areas denote Novices. Squares are households. Occurrences of female cat groups are denoted. Circles are barns or other buildings used by cats.

Fig. 10 A. The situation in 1978.

B : 1979

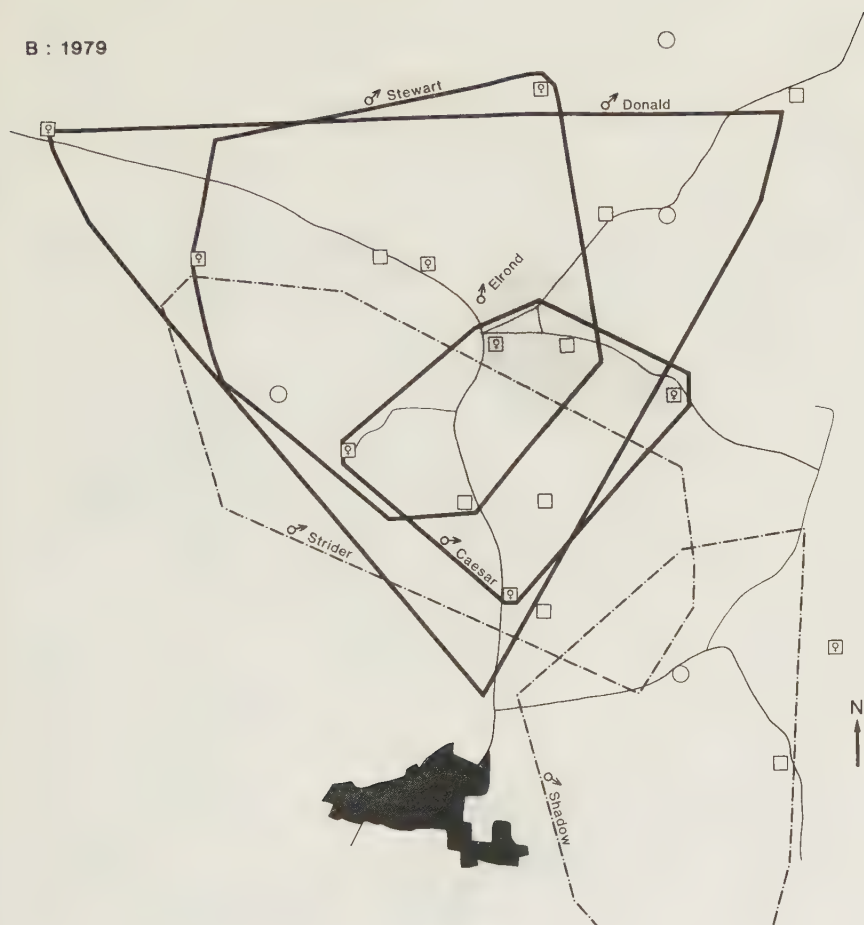


Fig. 10 B. The situation in 1979. Hatched area denotes home range of Challenger Elrond.

C:1980

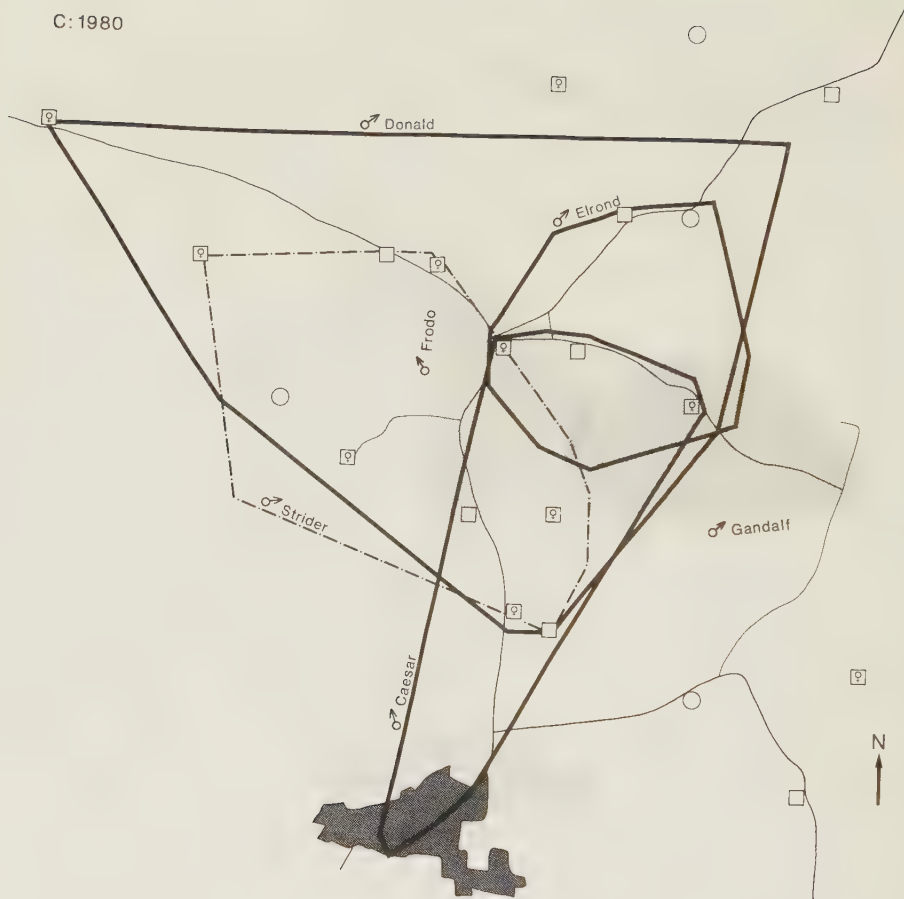


Fig. 10 C. The situation in 1980.

TABLE 11

Scent marking frequencies during travelling and during other activities in four categories of male cats. Only observations made in Jan-Sep were considered. Sniff/mark ratio was based only on observations, where it clearly could be seen whether or not the cat investigated the marking plan before marking itself.

		Novices	Outcasts	Challengers	Breeders
<u>Travelling</u>	minutes				
	observed	76	144	95	546
	N Scentmarks				
	observed	18	29	21	200
	Scentmarks				
	per hour	14	12	13	22
<u>Other</u> <u>acti-</u> <u>ties</u>	minutes				
	observed	123	1010	751	1265
	N Scentmarks				
	observed	1	2	3	30
	Scentmarks				
	per hour	0.5	0.1	0.2	1.4
Ratio sniffs per scentmark		1.1 (19/17)	N.D.*	N.D.*	0.5 (78/143)

*N.D. = not sufficient data.



Fig. 11. Location points of Strider and Donald in 1979-80, where under "activity type" was recorded "travelling".



Fig. 12. Locations of scent marks (arrows), deposited during a travel by Donald between 11⁵⁰ and 15¹⁵, June 18, 1980 (the western dashed line), and by Elrond between 07⁵⁰ and 10²⁰, April 17, 1981 (the eastern dashed line). Dotted lines indicate sections of the movements when the cats were out of sight. Thick line denotes home range of Elrond. Donald's home range includes most of the map.

DISCUSSION

FACTORS INFLUENCING SOCIAL DOMINANCE

Social dominance should be used to maximize fitness, and it has to be backed up by real power. The results presented in this paper support these two statements. Male cats were competing with each other for mates. Those that managed to dominate their rivals had a higher reproductive success. Dominance was achieved by winning contests, in which probably both physical and mental power were important. These two sides of power were brought about by a combination of mature age, that brings mental factors like experience and self-confidence, and large size (= bodyweight) that is the base for physical strength. Both seems to be necessary for a male to reach high social rank. Frodo had the typical weight of a Breeder when one and a half years old, but remained a Novice for at least another one and a half year. Strider weighed only four kg in spring 1981, and had not yet attained Breeder status, although he was at least four years old by then.

Influence of bodyweight and age on social rank has been shown for many species, e.g. stoat Mustela erminea (Erlinge 1977a), and chipmunk Tamias striatus (Brenner et al. 1978). In the theory of sexual dimorphism with larger males in polygynous species, the assumption that large size increases ability to compete successfully for mates, is essential (e.g. Crook 1972, Trivers 1972, Halliday 1978). Also theory of asymmetric contests assume body size as an important cue for assessment of "resource holding power" (Parker 1974). Parker (op. cit.) also argued that if long time damage might occur as a result of escalated contests, than young animals should withdraw, as their lifetime fitness would be more reduced through such damage, than older animals. The last argument, in a little different form, was also used by Selander (1965) to explain why delayed social maturation would occur in species who compete strongly for breeding opportunities. The male cats in the present study had a delayed maturation, both in a physical and a social sense.

There was a site dependency in social dominance among the present male cats. Apart from individual cases of reversed dominance relations, also the whole system of male cats holding Breeder status in some female groups, but not in others, within their home ranges, shows the influence of location on social rank. This is known from many other species, e.g. Stellers Jay Cyanocitta

stelleri (Brown 1963) and chipmunk (Dunford 1970). Actually the whole concept of territoriality rests on variation of dominance with location. The reason behind this phenomenon could be an imbalance between holder and challenger in "pay-off" (Parker 1974), or the possession of a dominant position at a certain place could be used as an "uncorrelated" asymmetry to settle a contest (Maynard-Smith and Parker 1976).

ATTAINING BREEDER STATUS

Novices and Outcasts achieved Breeder status by going through the Challenger stage. The change from an avoiding and defensive behaviour to a challenging attitude probably was a result of growing physical strength and increasing experience and self-confidence. It was a more gradual process, than the absolute categorizing into well defined stages indicates.

The Breeder status can be reached in different ways, depending on the situation. In the present study, two different paths of development were observed in the two males that were followed through the entire succession from Novices to Breeders: One (Elrond) was a Challenger in both his own home household (The Center) and in a neighbouring household, and concentrated his efforts on these two female groups. When the resident Breeder (Caesar) left, Elrond immediately attained Breeder status in both groups. The other cat (Donald) did not have any females in his own household, and he seemed to adopt a trial and error behaviour. His home range as Challenger was four times larger than Elrond's, and he visited all female cat household in "The Core" and at least two outside in 1978, when he was classified as a Challenger. In 1979, he was classified as a Breeder, but actually a rather weak one, since he only maintained tenure in one female group for only part of the season. Also this year he visited most female groups in the area, and had an even larger home range than the year before. But when in 1980 he definitely attained Breeder status, he reduced his range. Elrond on the other hand, extended his range after becoming a Breeder, a tendency that continued in 1981 (Liberg unpubl.). Therefore, it is probable that the further development of these two males would converge towards the typical Breeder strategy with extra female groups, regularly visited, but not included in the dominion. This will be discussed further in the next section.

Here, I will try to answer two critical questions about the strategies of Breeders.

A) Why do not Breeders maintain exclusive territories?

B) Why do Breeders incorporate a larger number of female groups in their dominions, than they can control completely?

A) Why do not Breeders maintain exclusive territories?

Three forms of polygyny have been described (Emlen and Oring 1977):

1. Resource defence polygyny: Males control access to females indirectly by monopolizing critical resources.
2. Female (or harem) defence polygyny: Males control access to females directly, usually by virtue of female gregariousness.
3. Male dominance polygyny: Males or critical resources are not economically monopolized. Males aggregate during the breeding season and female select mates from these aggregation.

The present cat population belonged to the form II polygynous system with males taking advantage of the clumping of females who were aggregated for other reason than for reproduction. But Breeders did not keep complete control of access to females, and they did not maintain exclusive territories. Brown (1964) argued that aggressive defence of a resource and territorial behaviour evolves only when the critical resource is economically defendable. A clumped and predictable resource like a group of female house cats at a household would seem to be economically defendable. And indeed, there was some evidence of territorial defense. Breeders attacked other adult males, not only while courting oestrus females, but also at other times, and even at places far from nearest female cat. They also had some success in evicting potential competitors from their dominion. Many Novices emigrated, obviously in response to aggression from other male cats, especially Breeders. And Outcasts settled in areas away from the resource the Breeder defended, the female group. Outcasts that included female cat households in their ranges, tended to keep away from the neighbourhood of these households whenever a female was in oestrus there. But still the dominions of Breeders were not exclusive, but overlapped with the most competitive rivals, other Breeders. To try and understand the strategy of the territorial defence that seemed to occur, I will look at the situation

from the intruders' point of view.

For an intruder the gain that might be achieved by trespassing in a defended area should be weighed against the cost if detected by the defender. Also involved are the probabilities of achieving the pursued gain, and of being detected by the defender. For a passerine bird where territories are small, the cost if detected does not seem to be high (it is chased away) but the probability of being detected must be close to one. This also influences the probability of achieving the aim with the intrusion, which must be low in this case. Therefore, the net gain probably is below zero, even though the cost of intrusion was low. The situation is reversed for less mobile animals with large territories, but dangerous weapons like large carnivores. The probability of being detected is low, but the cost, if detected, might be high. Different aims with the trespassing of course yields different net benefits. The fitness gain for a trespassing male is higher if a receptive female is found, than if just a prey animal is caught. But the risk of being detected is probably much higher in the former case. The probability that the territorial male is close to the female in oestrus, is much higher, than that he should happen to be present in exactly the same area as any certain prey animal. This could explain the overlap of male home ranges in some solitary polygynous carnivores expected to be territorial (Seidensticker et al 1973, Erlinge 1977b). If trespassing for hunting has a high net benefit, but trespassing for mating has a low net benefit, territorial males might have responded by not defending hunting rights, and only defend mating rights.

If we then again go back to the present cat population, here male trespassing seems to have a positive net gain, even when the aim is to mate. The probability of being detected is lower than in the passerine case, but higher than in the carnivore case. The cost if detected, is moderate. Male cats rarely get seriously wounded in fights. The possible gain in fitness on the other hand is high, and probability of attaining it, is also relatively high. So trespassing should pay. But then we are left with the problem why Breeders have not adapted to this strategy, and given up territorial defence completely. The answer could be, that they actually are keeping the defence on the most economic level (Fig. 13).

If we assume that the purpose of trespassing is to mate with

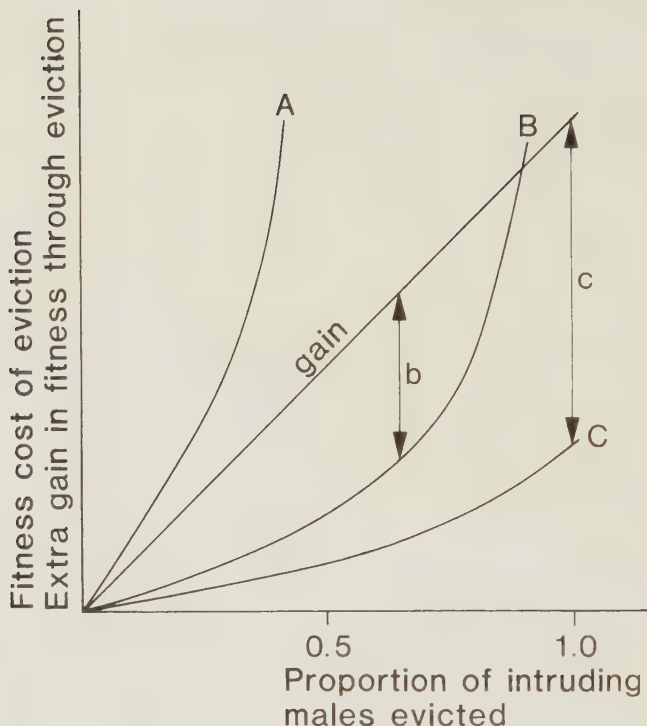


Fig. 13. A model for a male animal's defense of a territory to control access to females living inside the territory. If there are a number of potential male intruders that all have the same probability of mating with a female, then the gain for the territory holder would increase at a constant rate in proportion to the number of intruders evicted. However, if the cost per eviction is not constant, either because some intruders take less effort to detect than others, or are stronger (hold a higher RHP, Parker 1974), then the cost function should increase at an increasing rate. There are three principal forms that the cost function may take in relation to the gain function. One is represented by A, where no territorial defense should occur. Another is represented by B, where the highest net gain, *b*, is achieved by evicting a portion of the intruders, and finally there might be a cost function C, where the highest net gain is achieved when all intruders are evicted. In this case the territory should be kept exclusive.

females, and each trespasser have the same probability of finding a female and mating with her, than the benefit of eviction should be increasing linearly with proportion of trespassers evicted. But it is likely that the cost of eviction is low for low-ranking males, e.g. Novices, where the asymmetry in RHP (Maynard-Smith &

Parker 1976) is large, but that the cost per intruder expelled increases as the defender meets increasingly stronger opponents. Also, the fewer antagonists that are left in the territory, the smaller is the probability of an encounter with any one of them. This model fits well with data. As already mentioned, the Breeder actually managed to evict or keep out a certain number of males, usually Novices and Outcasts with low RHPs.

Scent marking was frequent in the present cat population, but marks did not deter trespassers. If the marks are individually recognizable, which I have no doubt of, then the receiver of the message will know whether he has met the donor before, and what chances he might have to win a contest if they meet again. This explains why low ranked individuals mark less frequently, but check other marks more frequently than high ranked. Actually it is a little surprising, that these cats mark at all, as it would seem best for them not to be noticed at all. The answer could be self assurance. But there might be something more going on with scent marks. It has become increasingly clear, that animal signals not only, or even mainly, convey correct information, but rather serve to manipulate other individuals (Charnow & Krebs 1976, Dawkins and Krebs 1978). There is no reason to believe that scent marks should be excepted from deceit and manipulation.

B) Why do Breeders include more female groups in their dominions, than they can control?

Most Breeders included more female group in their range than they actually controlled as Breeder. They regularly visited foreign Breeders' groups and courted females in oestrus. If the resident Breeder was present, they assumed a PM position, if they were not chased off. At the same time, they did not control access to their "own" female group completely. Coat colour inheritance data showed that Breeders did not sire all litters born in their dominions. It was also observed that subordinate males mated with females in the absence of the Breeder. In some of these cases it was known that the Breeder was occupied with a female in oestrus in another group at the same time.

It might be, that Breeders actually obtained more mating opportunities in this way. However, some data and theoretical considerations point to another reason for this behaviour. If inbreeding costs are high as they have been shown to be in some studies (Bulmer 1973, Greenwood et al. 1978, Packer 1977 (cited in Bert-

ram 1978)) then Breeders should avoid incest. After the first year of tenure in a female group, the probability of mating with daughters increases with each extra year of tenure.

The Breeder could restrict his mating to the older unrelated females only, or he could leave the group altogether. In both cases the advantage of extending his activity to a large number of female groups appears evident. A Breeder that gradually makes acquaintance with and incorporates new female groups in his dominion even if this means he can not control them completely, can also gradually give up groups where the inbreeding level is building up. This could have been the reason for Caesar leaving the Center and Eastwood groups in 1980. In the Center group he was probably father of half the adult females by then. A similar case was also observed in another part of the "Population Study Area" in 1976, where a dominant male, probably a Breeder, took over several female groups from another Breeder that died, and left some of his old groups (Liberg 1980).

This is a problem that the male cat shares with most longlived polygynous males controlling the same group of females during several breeding seasons. In mountain lions, resident breeding males shifted home ranges in a pattern similar to that described here (Seidensticker et al. 1973).

In lion, incest avoidance is a by-product of a rather rapid turn over of pride males (Bertram 1978). In African wild dog, subordinate females usually leave the pack (Frame et al. 1979) as is the case in several primates (Harcourt et al. 1976, Pusey 1980). In wolves, if one α -animal dies, the survivor mates with one of the subordinate pack members, in spite of the fact that the new mate most certainly is a close relative. (Mech 1970 and pers. comm.). This might be a case, where the cost of incest avoidance, i.e. emigration, is higher for the dominant animal, than the cost of inbreeding (Bengtsson 1978).

There were some indications that incest avoidance was not so important in the present cat population. Both Caesar and Elrond stayed to breed in their own maternal group. If inbreeding for ecological reasons has occurred for a long time in domestic cats, than its costs at present might be low, as most deleterious genes already are weeded out (Bengtsson 1978). However, there might be other reasons why a Breeder leaves his old groups, and, therefore, benefits from a gradual take-over of new groups. One is that he simply gets evicted from some of his groups by a stronger Chall-

enger or a neighbouring Breeder. Another could be if inbreeding costs really are low. Then the Breeder might give up old groups voluntarily, to let a son take over the Breeder status. The observation of the Breeder Elrond just lying by, letting the younger groupmate Gildor court and copulate with a female belonging to Elrond's dominion, without interference, could indicate such a strategy.

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(Appendix on next page!)

APPENDIX I

Basic data for calculation of Breeder status of male cats in the various female cat groups in "The Core". The three conditions (C1, C2, C3) that should be satisfied (given in Methods) are denoted by + if satisfied, and - if not satisfied. The conditions are denoted in the same order as given in Methods. If the cat was classified as a Breeder in a female group, there is given a 1 after the three conditions (under B), otherwise there is a 0. Shared Breeder status is denoted by $\frac{1}{2}$, but when summing up they are counted as one.

	Eastwood			Center			Offside			School			Meadow			Watermill			Marsh			Highway			Breeder status in total groups
	C1	C2	C3	B	C1	C2	C3	B	C1	C2	C3	B	C1	C2	C3	B	C1	C2	C3	B	C1	C2	C3	B	
1978																									
Caesar					+	+	+	1		+	+	+	1	+	+	+								3	
David					+	-	-	0		-	-	0	-	-	-	0								0	
Donald					+	-	-	0		+	-	0	+	-	-	0								0	
Elrond					+	-	-	0		-	-	0	-	-	-	0								0	
Stewart					-	-	-	0		+	-	0	-	-	-	0								0	
Sam					-	-	-	0		-	-	0	+	-	-	0								0	
1979																									
Caesar	+	+	1		+	+	-	$\frac{1}{2}$		-	-	0		+	+	-					+	?	?	?	2
Donald	+	-	0		+	-	-	0		+	-	0		+	+	-					+	-	-	?	1
Elrond	+	-	0		+	-	-	0		-	-	0		-	-	0					-	-	-	0	0
Stewart	-	-	0		+	+	+	$\frac{1}{2}$		+	+	1		+	+	+					-	-	-	0	3
Strider	-	-	0		-	-	-	0		-	-	0		+	+	-					+	?	-	0	0
Frodo	-	-	0		+	-	-	0		-	-	0		-	-	0					-	-	-	0	0
Faxe	-	-	0		-	-	-	0		-	-	0		-	-	0					-	-	-	0	0
Shadow	-	-	0		-	-	-	0		-	-	0		-	-	0					-	-	-	0	0

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C O N T E N T S

List of papers	2
Preface	3 - 4
Summary of the results, and discussion of adaptations of the cat to symbiosis with man	5 - 12
Spacing patterns in a population of rural free roaming domestic cats	13 - 26
Food habits and prey impact by a rural domestic cat population in southern Sweden	27 - 56
Hunting efficiency and prey impact by a free roaming house cat population	57 - 67
Courtship behaviour and sexual selection in the domestic cat	69 - 87
Reproductive success in male cats in relation to social status	89 - 135